# SYSTEMATICS OF SNAKES OF THE *DIPSAS OREAS* COMPLEX (COLUBRIDAE: DIPSADINAE) IN WESTERN ECUADOR AND PERU, WITH REVALIDATION OF *D. ELEGANS* (BOULENGER) AND *D. ELLIPSIFERA* (BOULENGER)

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ABSTRACT. The systematics and biology of colubrid snakes from western Ecuador and northern Peru in the *Dipsas oreas* group, comprising the nominal taxa *D. oreas* (Cope), *D. elegans* (Boulenger), and *D. ellipsifera* (Boulenger), are reviewed. The last two species are resurrected from the synonymy of *D. oreas.* These species, especially *D. elegans* and *D. ellipsifera,* have been confused in previous literature because of inadequate attention to patterns of sexual dimorphism and geographic variation. *Dipsas elegans* and *D. ellipsifera* share a distinctive color pattern that is quite different from color patterns in *D. oreas. Dipsas ellipsifera* differs from both *D. oreas* and *D. elegans* in having lower ventral and subcaudal counts, but sexes must be analyzed separately to see the distinctions clearly. Other subtle characters of scutellation, coloration, and dentition aid in distinguishing these species. *Dipsas elegans* is unusual in that males have significantly more ventral scutes than females, the reverse of the more common colubrid pattern of sexual dimorphism, in which females have more ventrals than males; neither *D. oreas* nor *D. ellipsifera* is sexually dimorphic for this character.

*Dipsas ellipsifera* is known only from the valley of the Río Mira in extreme northwestern Ecuador (Imababura Province). *Dipsas elegans* is known from the western versant of the Andes in Ecuador from just north of the equator to about latitude 2°S; it is also found in the inter-Andean valley of the upper Río Guayllabamba east of Quito. *Dipsas oreas* is known from southern Chimborazo and Guayas Provinces south to Loja Province in southern Ecuador, thence south along the western slopes of the Andes to at least the Río Zaña (6°51′S) in northern Peru. The occurrence and distribution of *D. oreas* in Peru is detailed for the first time. Most localities for *D. oreas* are on the Andean slopes, but the species is also recorded by specimens from the lowlands in the vicinity of Guayaquil, Ecuador. The type locality of *D. oreas* and many other South American amphibians and reptiles obtained by the naturalist James Orton is the "elevated Valley of Quito," which has been errone-

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ously interpreted narrowly as the vicinity of Quito, Ecuador. Orton's own writings show that a broader interpretation encompassing virtually all of the Ecuadorian highlands was intended. The ranges of *D. elegans, D. ellipsifera,* and *D. oreas* are very likely extremely fragmented because of significant destruction of forest habitats in western Ecuador and Peru.

Hemipenes of *Dipsas elegans, D. ellipsifera,* and *D. oreas* are slightly bilobed, fully capitate, and have ornamentation similar to other species of the tribe Dipsadini (*Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas*). The capitulum is ornamented with papillate calyces and the sulcus spermaticus bifurcates within the capitulum. Proximal to the capitulum a battery of enlarged spines encircles the midsection of the organ. A large basal nude pocket is present on the hemipenis in all three species.

Notes on coloration, natural history, and behavior are reported for the three species of the *oreas* group, although most observations are for *Dipsas oreas.* In northern Peru, *D. oreas* shows extensive intrapopulational variation in coloration, which could in part be sexually dimorphic. It is unclear whether this variation pertains to other parts of the distribution. *Dipsas oreas* is active nocturnally in low vegetation but seeks seclusion in leaf litter or under surface objects on the ground during the day. This diel behavior pattern is also reported for several other species of *Dipsas* and might be common in the genus. In northern Peru, the activity of adult *D. oreas* is strongly seasonal and coincides with the rainy season. A peculiar aggregation of *Dipsas oreas* encountered at a locality in northern Peru is described. Comprising one female and six males, this is the first reported case of "aggregation behavior" in any snake of the tribe Dipsadini and one of very few observations of such behavior in Neotropical colubrids. Details of the aggregation suggest an association with mating, and the existence of communal nesting in this species suggests that aggregation might occur for oviposition as well.

A key to all species of *Dipsas* reported or expected in western South America (Colombia, Ecuador, and Peru) is provided. This includes six species known from western Ecuador (*andiana, elegans, ellipsifera, gracilis, oreas,* and *temporalis*), two of which (*gracilis, oreas*) also occur in western Peru, and three additional species known or expected in Chocoan Colombia (*nicholsi, sanctijohannis,* and *viguieri*). *Dipsas gracilis* and *D. viguieri* are not distinguishable by any reported characteristics of the taxa. Brief notes are provided on the occurrence of *D. gracilis* in northwestern Peru. Some taxonomic issues concerning two species of the Amazonian versant, *D. latifasciata* and *D. latifrontalis,* are outlined. These species are not clearly distinguishable on the basis of characters discussed in the literature, and the assignment of these names to specimens from eastern Ecuador needs to be reviewed in conjunction with study of their holotypes.

RESUMEN. Se revisan la sistemática y biología de las serpientes de la familia Colubridae de Ecuador occidental y el norte del Perú en el grupo *Dipsas oreas,* que se compone de los taxones nominales *D. oreas* (Cope), *D. elegans* (Boulenger), y *D. ellipsifera* (Boulenger). Las últimas dos especies se resucitan de la sinonimia de *D. oreas.* Estas especies, especialmente *D. elegans* y *D. ellipsifera,* se confusaron en la literatura anterior debido a insuficiente atención a los patrones de dimorfismo sexual y la variación geográfica. *Dipsas elegans* y *D. ellipsifera* comparten un patron de colores bien distinto y substantivamente diferente de los patrones en *D. oreas. Dipsas ellipsifera* es distinto de *D. oreas* y *D. elegans* al tener bajos cuentos de ventrales y subcaudales, pero es necesario analizar por separado los sexos para ver claramente las distinciones. Otros carácteres más sutil de la escamación, la coloración, y la dentición ayudan al distinguir estas especies. *Dipsas elegans* es extraño ya que los machos tienen considerablemente más escamas ventrales que las hembras, lo contrario del patrón común de dimorfismo sexual en la familia Colubridae, en que las hembras tienen más ventrales que los machos; ni *D. oreas* ni *D. ellipsifera* demuestra dimorfismo sexual en esta carácter.

*Dipsas ellipsifera* se conoce solamente del valle del Río Mira al norte extremo del Ecuador (Provincia de Imbabura). *Dipsas elegans* se conoce del lado occidental de los Andes en Ecuador desde justo al norte del ecuador hasta aproximadamente la latitud 2°S; se encuenta también en el valle interandino del alto Río Guayllabamba al este de Quito. *Dipsas oreas* se conoce desde la parte sur de las provincias Chimborazo y Guayas hasta la provincia Loja en el sur de Ecuador, desde allí a lo largo de las vertientes occidentales de los Andes, por lo menos hasta el Río Zaña (6°51′S) en el norte de Perú. La presencia y distribución de *D. oreas* en Perú se detallan para la primera vez. La mayoría de las localidades para *D. oreas* se encuentra en las vertientes Andinas, pero también es recordado por ejemplares de tierras bajas vecino a Guayaquil, Ecuador. La localidad típica de *D. oreas* y muchas otras especies de anfibios y reptiles sudamericanos que fueron obtenido por la naturalista James Orton es "el valle elevado de Quito", que se han interpretado estrechamente y equivocadamente como los alrededores de la ciudad de Quito, Ecuador. Las obras propias de Orton demuestran que el quisó decir una interpretación más amplia, que abarcó casi todas las partes altoandinas Ecuadorianas. Los rangos de *D. elegans, D. ellipsifera,* y *D. oreas* son probablemente muy fragmentados debido a la destrucción substantiva de los bosques en Ecuador y Perú occidental.

Los hemipenes de *Dipsas elegans, D. ellipsifera,* y *D. oreas* son ligeramente bilobulados, completamente capitatos, y tienen ornamentación similar a otras especies del tribo Dipsadini (*Dipsas, Sibon, Sibynomorphus,* y *Tropidodipsas*). El capítulo es ornamentado con cálices que llevan papilas, y el surco espermático se divide dentro del capítulo. Proximal al capítulo hay una serie de espinas agrandadas que rodean el órgano. Un bolsillo desnudo y grande se encuentra en la base del hemipene de las tres especies.

Se reportan notas sobre la coloración, la historia natural, y el comportamiento para las tres especies del grupo *oreas,* aunque la mayoría de las observaciones son para *Dipsas oreas.* En el norte de Perú, *D. oreas* muestra mucha variación intrapoblacional en colores. En parte, esta podria ser debido al dimorfismo sexual. No es claro si esta variación pertenece a otras partes de su distribución. *Dipsas oreas* es activo nocturnamente en vegetación baja, pero por día se encuentra en la hojarasca o debajo de objetos sobre la superficie de la tierra. Este patron de comportamiento diario se reporta para varias otras especies de *Dipsas* y puede ser común en el género. En el norte del Perú, la actividad de adultos de *D. oreas* es muy estacional y corresponde fuertamente con la época de lluvias. Se describe una agregación extraña de *Dipsas oreas* que se halló en una localidad de campo en el norte del Perú. Compuesto de una hembra y seis machos, esto es el primero reporte de "comportamiento de agregación" en una especie del tribo Dipsadini y es uno de muy pocas observaciones de tal comportamiento en colubrideos Neotropicales. Los detalles sugeren que la agregación fue asociada con el acoplamiento y la existencia de nidos comunales en esta especie sugere que agregación puede suceder también por poner huevos.

Se provee una clave para todas las especies de *Dipsas* conocidas o esperadas en Sudamérica occidental (Colombia, Ecuador, Perú). Estas incluyen seis especies conocidas del Ecuador occidental (*andiana, elegans, ellipsifera, gracilis, oreas, temporalis*), de las cuales dos (*gracilis, oreas*) también se encuentran en el Perú occidental; se conocen o se esperan tres especies adicionales en el Chocó de Colombia (*nicholsi, sanctijohannis, viguieri*). No se pueden distinguir *D. gracilis* y *D. viguieri* por las características reportadas en la literatura. Se proveen notas breves sobre la presencia de *D. gracilis* en el noroeste del Perú. Se resumen algunos problemas acerca de la taxonomía de dos especies de la vertiente amazónica, *D. latifasciata* y *D. latifrontalis.* No se pueden distinguir estas especies por las características en la literatura, y es necesario revisar el uso de estos nombres para especimenes desde Ecuador oriental conjunto con estudio de los holotipos.

## INTRODUCTION

Neotropical snakes of the genus *Dipsas* (Colubridae: Dipsadinae: Dipsadini) were last comprehensively reviewed by Peters (1960a). Many South American species remain poorly known because they are represented by few specimens and/or they exhibit complex variation in characters, such as color pattern and scutellation, typically used to infer species limits in snakes. Several species in western Ecuador and Peru have been poorly characterized in existing literature, making species determinations of certain populations difficult. At the time that Peters (1960a) and Peters and Orejas-Miranda (1970) reviewed *Dipsas,* a few species were known from western Ecuador, but none was recorded from the western slopes of the Andes or Pacific lowlands in Peru. The availability of new material makes review of these species timely because of the confused state of the systematics of several species in western Ecuador and misapplied names to many specimens already in collections. A subsequent paper (Cadle, unpublished data) will review new material of the related genus *Sibynomorphus.*

Peters (1960a) and Peters and Orejas-Miranda (1970) thought that three species groups of *Dipsas* were represented in western Ecuador: (1) the *variegata* group, represented in western Ecuador by *D. variegata variegata* and *D. variegata nicholsi*; (2) the *oreas* group, represented by *D. oreas, D. ellipsifera,* and, as clarified later by Kofron (1982), *D. elegans*; and (3) the *articulata* group, represented in western Ecuador by *D. gracilis* and *D. temporalis.* Subsequent to Kofron's (1982) review, *D. elegans* and *D. ellipsifera* were recognized as subspecies of *D. oreas* (Orcés and Almendáriz, 1987). Until recently, none of these species was known from Peru, but Cadle and Chuna (1995) and Tello (1998) reported *D. oreas* and *D. gracilis,* respectively, from northern Peru. Species in the *variegata* and *oreas* groups, in particular, have presented complex systematic problems, resulting in numerous misidentified specimens (e.g., several unrelated species confused with *D. variegata*; Cadle and Myers, 2003). Consequently, several species within these groups from Ecuador and Peru have routinely been confused, prompting me to review these groups while identifying collections resulting from biological inventories in northern Peru.

Cadle and Myers (2003) reviewed the

"*Dipsas variegata*" group (*sensu* Peters, 1960a) in Panama and western South America. Their principal conclusions relevant to the identity of species of *Dipsas* in western Ecuador were (1) specimens from Ecuador previously referred to *Dipsas v. variegata* were misidentified specimens of *D. oreas, D. andiana,* or *Sibynomorphus petersi,* all of which are well known from western Ecuador, and (2) Ecuadorian specimens identified as *D. v. nicholsi* by Peters (1960a) are a distinct species, *Dipsas andiana* (Boulenger), a name resurrected from the synonymy of *D. oreas,* where it had been placed by Peters (1960a). Thus, no definitive records of *Dipsas variegata* are known from Panama, Colombia, Ecuador, or Peru, and the close relationship of *D. andiana* to *D. variegata* seems highly questionable. See Cadle and Myers (2003) for further details.

Cadle and Myers (2003) briefly characterized *Dipsas oreas* in diagnosing *D. andiana.* They examined specimens of the nominal taxa *elegans* and *ellipsifera* but left their relationship to *D. oreas* as an "open question" (Cadle and Myers, 2003: footnote 13). This paper extends their discussion of *Dipsas oreas* and evaluates the status of *D. elegans* and *D. ellipsifera.* In addition, I summarize natural history and behavioral observations for these species and provide a key for the identification of all species of *Dipsas* known or expected from west of the Andes in Colombia, Ecuador, and Peru.

## METHODS

*Localities: The Río Zaña Study Site.* Most of my observations on the natural history of *Dipsas oreas* in Peru are derived from field work conducted in the vicinity of Monte Seco (also known as Monteseco), a small town on the north side of the Río Zaña in western Cajamarca department, Peru (6°51′S, 79°6′W). Thus, it seems pertinent to make a few brief comments on this locality and others in northern Peru where *D. oreas* is known to occur.

In 1987 (early dry season: May–June) and 1989 (early rainy season: January) for a combined total of 11 weeks, I made herpetological collections in the Monte Seco region; some results from those surveys were reported previously (Cadle, 1989, 1991; Cadle and Chuna, 1995; Cadle and McDiarmid, 1990). In the late 1980s and early 1990s, humid montane forest covered the Andean slopes above Monte Seco from approximately 1,500 to 2,500 m, with an areal extent estimated to be 2,500 ha (Sagástegui et al., "2003" [2004]). Above 2,500 m in the immediate vicinity were tablelands and slopes that had been largely cleared of forests, although forest fragments still existed up to nearly 3,000 m. Specific survey sites at Monte Seco varied, and fieldwork sampled a wide elevation range concentrated between 1,200 and 2,500 m; less intense sampling was conducted down to 1,000 m and as high as 3,000 m. The primary focus of the field work was dense humid montane forest covering the mountain slopes, but other habitats, including agricultural land (coffee plantations, secondary forests) and open highland grasslands and bushlands, were also sampled. The known flora of Bosque Monte Seco comprises approximately 380 species of flowering plants and 40 species of pteridophytes (Sagástegui et al., 2004).

Wet and dry seasons at the Río Zaña Study Site are very pronounced, with a distinct rainy season occurring from approximately December to April. Temperatures recorded using a maximum/minimum mercury thermometer at the base camp (1,800 m) were as follows:

5 May–26 June 1987 (50 days, early dry season)
  Maximum daily average, 28.5° C
    (range 21.5°–35.5° C)
  Minimum daily average, 9.2° C
    (range 5.5°–12° C)

14–29 January 1991 (12 days, early rainy season)
  Maximum daily average, 19.5° C
    (range 16.5°–21° C)

Minimum daily average, 10.7° C
(range 10°–12° C)

The difference between the dry and rainy season maximum daily temperatures at the study site is because many days during the rainy season are prone to dense fog or cloud cover, whereas fog is rare during the dry season. These records show that the minimum daily temperature range was much greater during the dry season (characterized by clear, cool evenings) than during the rainy season (foggy/cloudy, warmer evenings), even though average minimum temperatures are similar.

Cadle (1989, 1991), Cadle and Chuna (1995), and Cadle and McDiarmid (1990) give additional details on the geography and habitats of the Monte Seco region. Dillon et al. (1995) included the humid forest of Monte Seco in a floristic study of western Peru and Ecuador, Sagástegui and Dillon (1991) provided a checklist of its flora, and Sagástegui et al. (2004) included the site in a comparative floral analysis of humid montane forests of northern Peru. For simplicity, in this paper I refer to all specific localities within the Monte Seco area as the Río Zaña Study Site and give elevation and habitat detail where pertinent. Descriptions or photographs of the Río Zaña Study Site and some other localities cited herein are given by Cadle (1991), Cadle and Chuna (1995), and Sagástegui et al. (2004). The herpetological collections made at the Río Zaña Study Site in 1987 and 1990 were timely, inasmuch as a considerable portion of the humid forest was cut and burned in the mid-1990s to provide pasturage for cattle and land for coffee production (see Sagástegui et al., 2004: figs. 6, 7). The site should be resurveyed to determine how much of its unique herpetofauna survives and to provide a baseline for its future recovery or extinction.

Elevations for my field sites were determined with a Thommen© altimeter, usually in conjunction with topographic maps. Coordinates and elevations for other localities, unless given by the collectors or otherwise stated, were derived from ornithological gazetteers of the Neotropics (Paynter, 1993, 1997; Stephens and Traylor, 1983); from Peruvian departmental maps or 1:50,000 topographic maps produced by the Instituto Geográfico Nacional, Lima; or from the online versions of the gazetteers of the U.S. Board on Geographic Names at the GEOnet© names server (http://earth-info.nga.mil/gns/html/index.html; the Web address seems to change with great frequency but should be searchable with the name GEONET). Bracketed data in localities are inferences from these sources. Abbreviations for museums in which cited specimens are housed are given in the list of specimens examined.

*Systematic Characters, with Special Reference to* Dipsas. I followed standard methods used in previous studies of snake systematics (e.g., Cadle, 1996; Cadle and Myers, 2003; Myers, 1974). Because some scutellation characters are highly variable intraspecifically within *Dipsas,* I here comment on the nature of the variation and ways in which some of these characters were recorded.

Peters (1960a: 25) noted the extreme variability of head scale patterns within *Dipsas*: "Division, extra suturing, or fusion takes place in nearly every head scale in this genus." Scale patterns of the temporal region in *Dipsas* are especially prone to intraspecific variation (Peters, 1960a: 26; Cadle and Myers, 2003: table 1), and the patterns of fragmentation and fusion of temporal scales make concise character definitions of species difficult. Generally, I attempted only to score primary and secondary temporals, and even this proved difficult in some cases. A few other head scale patterns seem useful in distinguishing some species pairs, especially when the frequencies of alternative states are considered. In this category are scales in the loreal region involving the loreal, postnasals, preoculars, and prefrontals; a few comments concerning scale patterns in this area are warranted because they are helpful in distinguishing species considered herein.

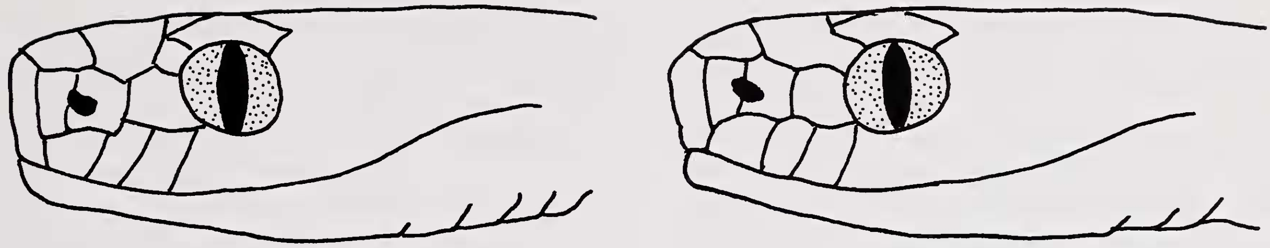
In those cases in which only a single scale is present between the postnasal scale and the eye, I follow Peters (1960a: 7–8) in considering this scale to be a loreal. A preocular scale, when present in *Dipsas,* is small, usually located superior to the loreal, and bordered by the loreal, prefrontal, supraocular, and eye (Fig. 1). This terminology is also consistent with definitions given by Savage (1973), but *Dipsas* differs from the more common colubrid conditions commented upon by Savage. Savage (1973: fig. 1) considered the common condition in which the preocular scale separates the loreal scale from the anterior border of the eye (i.e., the preocular is intercalated entirely between the eye and loreal); Savage also considered patterns of scale fusions involving the loreal + prefrontal. In contrast, in *Dipsas* the preocular typically lies superior to the loreal (Fig. 1), and the loreal contacts the anterior border of the eye; scale fusions usually involve the preocular + prefrontal.

Differences among the species of *Dipsas* considered herein involved primarily two characters of the loreal region: (1) the shape of the loreal scale itself, which was either square/polygonal or much longer than tall (rectangular), and (2) whether a preocular appeared as a distinct scale (usually superior to the loreal) or was fused with the prefrontal scale (in which case the fused prefrontal–preocular touches the anterior border of the eye). Four patterns in scales of the loreal region were most frequent, loreal patterns 1–4 (Fig. 1), distinguished by the two characters of the loreal and preocular scales just mentioned. In addition to these common patterns, a few rarer conditions were observed, which involved either the presence of a subpreocular (formed by a suture segregating the posteroventral corner of the loreal from the main part of that scale; loreal pattern 5, Fig. 1) or horizontal partition of the loreal, nasals, and/or prefrontals to form an unusually long preocular above the loreal (loreal pattern 6, Fig. 1).

Loreal patterns 1 and 2 are identical except for the presence or absence of a discrete suture separating the preocular scale from the prefrontal scale. Patterns 3 and 4 are related in a similar way. Usually a single pattern overwhelmingly predominated for each species (see Tables 1 and 3 and the discussion of *Dipsas oreas* for exceptions). In all cases of intraspecific variability in patterns 1–4, alternative states within a species were always either Patterns 1 and 2 or patterns 3 and 4 (and never, e.g., pattern 1 with pattern 4). For example, in *D. oreas,* in which pattern 2 was overwhelmingly frequent, alternate states involved pattern 1 or other rare patterns, but never patterns 3 or 4. Patterns 5 and 6 appeared with less frequency than any other patterns, except for a high frequency of pattern 6 within one population of *D. oreas* (see below).

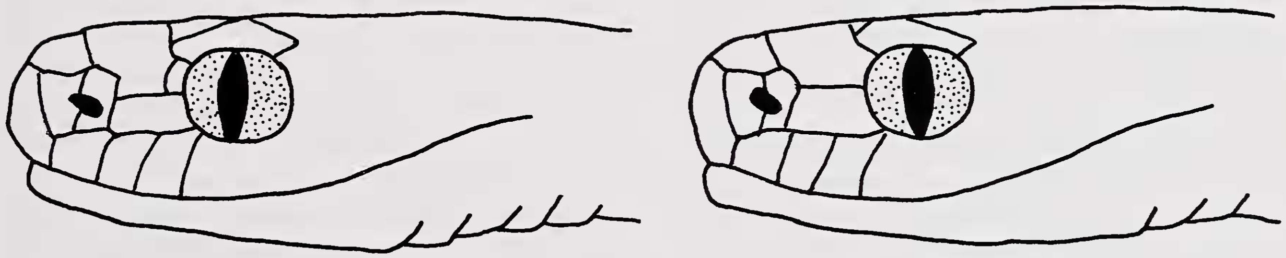
One reviewer of this paper suggested including total segmental counts (ventrals + subcaudals) as part of the diagnoses and descriptions of these species, and as a summary to aid in sexing of specimens (the idea being that total segmental counts would add together whatever smaller sexual dimorphism might exist within ventral or subcaudal counts considered separately, thus enhancing the distinction between sexes). This would perhaps permit easier sexing of specimens without the need for dissection. Although this approach seems useful for some groups of snakes, several aspects of variation within the snakes considered herein make the use of total segmental counts less useful, and exclusive consideration of total counts actually obscures some patterns apparent from consideration of ventral and subcaudal counts separately.

Two of the species considered herein (*Dipsas oreas* and *D. ellipsifera*) are not at all sexually dimorphic in ventral counts, but strongly dimorphic in subcaudal counts (male counts higher than female counts with virtually no overlap in counts



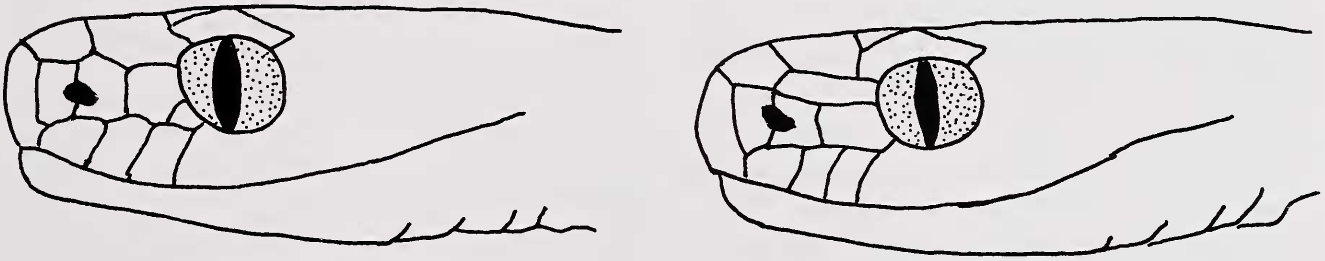
**Loreal Pattern 1**

**Loreal Pattern 2**



**Loreal Pattern 3**

**Loreal Pattern 4**



**Loreal Pattern 5**

**Loreal Pattern 6**

Figure 1. Variation in scale patterns in the loreal region of species of *Dipsas*. **Patterns 1 and 2:** loreal squarish or polygonal; separate preocular present above loreal (pattern 1) or fused with prefrontal scale (pattern 2). **Patterns 3 and 4:** loreal rectangular, much longer than tall; separate preocular present above loreal (pattern 3) or fused with prefrontal scale (pattern 4). **Patterns 5 and 6:** rare patterns; pattern 5 is similar to pattern 2 but has a small triangular preocular separated from the posteroventral corner of the loreal; pattern 6 has an elongate preocular above the loreal and extending from the eye to the internasal. Patterns 1 and 2 are the common patterns in *D. oreas,* with patterns 5 and 6 less frequent. Patterns 3 and 4 are characteristic of *D. elegans* and *D. ellipsifera*. See text for discussion.

between the sexes; see Tables 1–3). In these species, use of total segmental counts yields no insights that are not apparent from separate consideration of ventral and subcaudal numbers, specifically because the difference between the sexes with regard to total segmental counts is contributed entirely by the subcaudals; this fact is obscured when the subcaudal count is evaluated solely as a component of the total segmental count. On the other hand, in *D. elegans,* males have significantly greater numbers of ventrals and subcaudals than females, with virtually no overlap in the counts for either character between the sexes. As in *D. oreas* and *D. ellipsifera,* the use of total segmental counts in *D. elegans* reveals nothing that would not be seen by separate consideration of ventrals and subcaudals, each of which is strongly sexually dimorphic for this species. Moreover, it obscures the highly unusual pattern of sexual dimorphism in ventral counts in *D. elegans* (discussed later herein).

Thus, the use of total segmental counts elucidates no patterns of sexual dimorphism or interspecific differences within the *Dipsas oreas* group that would not be evident from separate analysis of ventral and subcaudal numbers. It also potentially obscures other features, such as the relative contribution of ventrals or subcaudals to any revealed pattern, and atypical patterns of sexual dimorphism (as for *D. elegans*). Nonetheless, I report total segmental counts in the descriptions and summary data tables that follow so that others can evaluate their utility for themselves. Whether the approach of using total segmental counts yields generally useful insights into the systematics of *Dipsas* is not clear to me. A casual inspection of data for several other South American species (Table 4; unpublished data) indicated no particular utility over and above separate consideration of ventral and subcaudal counts for this small sampling of taxa.

## THE *DIPSAS OREAS* COMPLEX: RESURRECTION OF *DIPSAS ELEGANS* AND *DIPSAS ELLIPSIFERA*

Cope (1868) described *Leptognathus oreas* from a specimen (holotype: ANSP 10115) obtained by James Orton with the type locality "elevated Valley of Quito" [Ecuador]. The "Valley of Quito" is the type locality for many amphibians and reptiles from Orton's large South American collections, but it has been misinterpreted by most authors dealing with his collections. It is clarified herein (see the account for *Dipsas oreas*).

Subsequent to Cope's description of *Dipsas oreas,* several taxa now perceived as related to it were described: *Leptognathus andrei* Sauvage (1884) with type locality "Loja, Nouvelle-Grenade"[2]; *D. elegans* (Boulenger, 1896) with type locality "Tehuantepec" [Mexico];, and *D. ellipsifera* (Boulenger, 1898) with type locality "Ibarra" [Ecuador]. These nominal taxa have remained poorly known since their descriptions. Peters (1960a) placed *D. elegans* and *D. ellipsifera* in his *oreas* group, but he had insufficient data to infer the relationships of *Leptognathus andrei.* Kofron (1982) provided photographs of the holotypes or syntypes of these forms and presented evidence that *Leptognathus andrei* Sauvage is a synonym of nominotypical *D. oreas,* a conclusion with which I concur on the basis of the photograph of the type and information provided by Kofron (see Table 3).[3]

The status of the nominal forms *Dipsas elegans* and *D. ellipsifera* and their relationship (if any) to *D. oreas* require further consideration. Contrary to reports in the literature, these three taxa are diagnosable from one another. Peters (1960a) recognized the similarity of the color patterns of *D. elegans* and *D. ellipsifera* but thought, erroneously, that *D. elegans* was a Mexican species because the original description (Boulenger, 1896: 452) stated that the holotype was from "Tehuantepec." Consequently, Peters assigned all Ecuadorian specimens with the distinctive *elegans–ellipsifera* pattern to *D. ellipsifera* (Peters, 1960a: 92). Peters' concept of *D. ellipsifera* therefore included specimens of *D. elegans,* even though he recognized the latter as a distinct species from Mexico. Subsequent discussions of these snakes (Kofron, 1982; Orcés and Almendáriz, 1987) have been misled by Peters' confusion of the two species in western Ecuador and by inadequate attention to sexual dimorphism and geographic origin of samples. This confusion, combined with tacit acceptance by most recent workers of specimen identifications in some older literature (e.g., Boulenger, 1896), has led to considerable uncertainty concerning differential characteristics of these nominal taxa and their respective distributions.

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[2] After 1830, New Granada comprised Panama + Colombia, a result of the secession of Ecuador and Venezuela from Gran Colombia, which had existed for a short time subsequent to colonial independence from Spain in the early 19th century. Sauvage (1884) reported "Nouvelle-Grenade" as the type locality, but the data recorded in the MNHN catalogues for the holotype (MNHN 6285) explicitly include "Loja" according to R. Roux-Esteve as reported by Kofron (1982: 48–49).

[3] *Dipsas oreas* was, for many years, also confused with *Sibynomorphus mikanii* (e.g., *Sibynomorphus mikanii oreas* or *Dipsas mikanii oreas* reported from Ecuador by Amaral 1929a, "1929"b [1930] and Parker [1934, 1938]). This resulted from synonymy of the two species by Günther (1872) and Boulenger (1896: 453). The confusion was discussed by Peters (1960a: 93–94).

Peters' (1960a) confusion of two Ecuadorian species under the name *Dipsas ellipsifera* affected his assessment of variation within this species. For example, his ventral and subcaudal counts for males and females of "*Dipsas ellipsifera*" (Peters, 1960a: 87) are exceptionally broad for a species of snake having a small range in western Ecuador. Nonetheless, Peters (1960a: 91) recognized a distinctive geographic pattern to the variation within his concept of *D. ellipsifera*:

> The material available can be divided into two groups as to provenance, the first coming from the Río Mira drainage and referred to as the "typical population," and the other from the western slopes of the Andes in Ecuador, to the south of the Río Mira. . . . Although the indicated differences between these two populations suggest subspecific status, I am not assigning them a name, because no satisfactory holotype is available. . . . The most striking differences between the two populations are in counts involving body segments.

Peters goes on to detail differences between the Río Mira specimens and the others when samples are segregated by sex. However, he did not make the conceptual leap to recognizing distinct species on the basis of these populational differences. Nor did he recognize that the "other" population from the western slopes of the Andes represented *Dipsas elegans*, believing as he did that *D. elegans* was a Mexican species.

Kofron (1982) clarified much of the confusion engendered by the uncertain origin of the holotype of *Dipsas elegans*. He summarized evidence that the holotype of *D. elegans* came from western Ecuador on the basis of the known travels and contacts of Adolphe Boucard, who sold the specimen to the British Museum (Kofron, 1982: 47). Kofron also reviewed the erroneous association of the name of the collector, François Sumichrast, who collected in the vicinity of the Isthmus of Tehuantepec, with the type of *D. elegans*. The error was promulgated by Günther (1885–1902: 141) and continued in checklists and faunal works (e.g., Peters, 1960a: 86; Smith and Taylor, 1945) until Kofron discovered the mistake. The unfortunate association of Sumichrast's name with the specimen that ultimately became the holotype of *D. elegans* resulted in it being considered a Mexican species by Peters (1960a) and others (e.g., Smith and Taylor, 1945).

Kofron's (1982) conclusion that the holotype of *Dipsas elegans* most likely came from Ecuador was a major step toward resolving the systematics of these snakes. Nonetheless, because the type specimens of *D. ellipsifera* and *D. elegans* have nearly identical color patterns, Kofron (1982: 48) synonymized *D. ellipsifera* with *D. elegans*, which is the earlier name. He did not thoroughly consider other character variation in available samples of these snakes, particularly in the context of geographic origin and sex, even though some of these patterns had already been elucidated by Peters (1960a; see previous quotation).

Despite having examined much of the same material as Peters, Kofron (1982) used Peters' (1960a) data when comparing the scale counts of the holotype of *Dipsas elegans* with *D. ellipsifera*, apparently failing to realize that Peters had confused the two species under the name "*Dipsas ellipsifera*" and overlooking Peters' more detailed discussion of geographic variation within his concept of *D. ellipsifera*: "The ventral and subcaudal counts of [the holotype of] *D. elegans* (183, 95) are within the ranges of 155–187 ventrals and 72–105 subcaudals reported for *D. ellipsifera* by Peters (1960)" (Kofron, 1982: 47). Thus, Kofron (1982) accepted Peters' (1960a) characterization of "*Dipsas ellipsifera*," which included specimens of *D. elegans*; not surprisingly, characteristics of the holotype of *D. elegans* conformed well to this composite taxon. Kofron did not reexamine the meristic data of specimens segregated by sex and locality and failed to notice a few other subtle differences between the two (see below). Peters (1960a), although he elucidated the pattern of geographic variation, did not differentiate the population samples as distinct taxonomic entities or associate the name "*Dipsas elegans*" with one of the population samples. Kofron (1982: 50) further suggested that "A comprehensive analysis of *D. oreas* and *D.* [*elegans*] may show the two to be subspecifically related, as I can distinguish the specimens . . . only by pattern." Kofron's (1982: 50) use of the name *D. ellipsifera* throughout the last paragraph of his text is an apparent lapsus for *D. elegans* in view of his synonymizing the former name with the latter earlier in the paper (Kofron, 1982: 48).

Orcés and Almendáriz (1987) acted on Peters' observations of geographic variation and examined additional specimens of both *Dipsas elegans* and *D. ellipsifera.* Unfortunately, in their reconsideration of the geographic pattern, they again lumped specimens by locality without regard to sex and thus failed to elucidate the correlation between sexual dimorphism in meristic data and geography that had been outlined by Peters (1960a). On the basis of average differences in meristic characters between population samples and little or no overlap in segmental counts between them, Orcés and Almendáriz (1987) maintained *D. elegans* and *D. ellipsifera* as distinct taxonomic entities but, following Kofron's (1982: 50) suggestion, considered them subspecies of *D. oreas* Cope. Orcés and Almendáriz provided the new combinations *Dipsas oreas elegans* and *Dipsas oreas ellipsifera.* The taxonomic justification was based on the broad overlap in ventral and subcaudal counts between nominotypical *D. oreas* and *D. elegans* (Orcés and Almendáriz, 1987: 138) and on the similar color patterns of *D. elegans* and *D. ellipsifera.*

The relationship, if any, of *Dipsas elegans* and *D. ellipsifera* to *D. oreas* warrants renewed scrutiny. Peters (1960a: 30–31) defined species groups on the basis of color pattern characteristics. This was unfortunate because color patterns are highly variable within some species of *Dipsas.* Nonetheless, Peters' *oreas* group included *D. elegans, D. ellipsifera,* and *D. oreas* by virtue of having a color pattern in which "the blotches are wider than the interspaces, with little contrast in color between them (pl. IVa) [and] the centers of the blotches are considerably lightened, which often gives the species an appearance of having paired ellipses on the sides. . . . The interspaces are rather heavily streaked and spotted with dark colors" (Peters, 1960a: 31).

A glance at the photograph that Peters chose to illustrate color patterns characteristic of the *oreas* group (Peters, 1960a: Plate IVa) shows that even this example does not fit the definition well (e.g., some of the interspaces are wider than the blotches and the the color pattern exhibits great contrast). Examination of only a few specimens will quickly erode confidence in Peters' definition of the *oreas* group. In all three species of the *oreas* group, the width of the blotches (or bands) varies along the length of the body; anteriorly, they are virtually always wider than the interspaces, but posteriorly, they are narrower than the interspaces. Most specimens of all three species have highly contrasting patterns (see later discussion of *D. oreas* for some exceptions, Cadle and Myers [2003: 21–25], the photograph of the holotype in Kofron [1982], and later discussion and illustrations herein).

The similarity and uniqueness of the color patterns of *Dipsas elegans* and *D. ellipsifera,* and their narrowly allopatric distributions (documented herein), suggest a close relationship between the two species. However, the similarity in segmental counts between *Dipsas elegans* and *D. oreas,* particularly among females (see Table 1), is of minimal consequence in assessing a possible relationship or conspecificity between them because many species of *Dipsas* have broadly overlapping scale counts (Cadle and Myers [2003] and subsequent discussions herein of *D. gracilis*). Thus, there seems to be little to unify *D. elegans, D. ellipsifera,* and *D. oreas* as a "species group," Peters' (1960a) color pattern characteristic notwithstanding. The color patterns of *D. elegans* and *D. ellipsifera* in reality bear little resemblance to that of *D. oreas.* Moreover, *D. andiana,* which Peters (1960a, 1965) considered a synonym of *D. oreas,* seems to be more closely related to *D. nicholsi* of Panama than to *D. oreas* (Cadle and Myers, 2003: 32–34). As emphasized by Cadle and Myers (2003), interspecific relationships among species of *Dipsas* need to be reassessed with a broader, more comprehensive set of characters than currently exists. Thus, the species groups elaborated by Peters (1960a) can be considered categories only of convenience.

Nonetheless, as will be shown, all three species of the *oreas* group are unusual with respect to sexual dimorphism in ventral counts compared with typical colubrid patterns. *Dipsas oreas* and *D. ellipsifera* show no sexual dimorphism in ventral counts, whereas *D. elegans* is highly unusual in that males have higher ventral counts than females. Whether these characteristics are restricted to the *oreas* group or are more broadly distributed within *Dipsas* requires study of additional species. A casual survey of data for other species of *Dipsas* at hand (Table 4 for *D. gracilis* and several species considered by Cadle and Myers [2003]) suggests that unusual patterns of sexual dimorphism in segmental counts might prevail within this genus. Thus, with respect to Peters' "*oreas* group," I address questions concerning the proper definition and diagnoses of the included species without necessarily implying any phylogenetic unity to the group.

Despite their previous confusion in much of the previous literature, careful study shows that *Dipsas elegans, D. ellipsifera,* and *D. oreas* can be distinguished from one another by a combination of scutellational, color pattern, and dentition characteristics. For these reasons I resurrect *D. elegans* and *D. ellipsifera* from the synonymy of *D. oreas,* and recognize all three taxa as valid species. I herewith provide differential diagnoses for these species and summarize their systematics, geographical distributions, and natural history. A summary of variation in standard systematic characters for these species (Table 1) will be helpful in following the ensuing diagnoses and descriptions.

## ***Dipsas ellipsifera* (Boulenger)**
## **Figures 2–8**

*Leptognathus ellipsifera* Boulenger, 1898: 117. Lectotype BMNH 1946.1.21.26 (Fig. 2, Table 2) designated herein. Type locality, "Ibarra" [Ecuador]. Werner, 1922: 197.

*Sibynomorphus ellipsifer*: Amaral, "1929"b [1930]: 197.

*Dipsas ellipsifera*: Peters, 1960a: 87. Peters, 1965: 3. Peters and Orejas-Miranda, 1970: 86.

*Dipsas elegans,* part: Peters, 1960a: 87, 91–92 (referred specimens from the western slopes of the Andes in Ecuador exclusive of those from the Río Mira drainage, specifically including those from "Camino a Mindo," "El Corazón," and "near Peñaherrera"). Kofron, 1982: 48. Miyata, 1982: 16.

*Dipsas oreas ellipsifera*: Orcés and Almendáriz, 1987: 138. Pérez-Santos and Moreno, 1991: 156.

### Notes on the Type Series and Designation of a Lectotype

The syntypes of *Leptognathus ellipsifera* comprise four specimens obtained by W. F. H. Rosenberg and sent to the British Museum of Natural History: BMNH 1946.1.21.26–29 (original numbers 98.4.28.87–90). The original description (Boulenger, 1898) simply noted "several specimens." Data on the syntypes are presented in Table 2, and the largest male, BMNH 1946.1.21.26 (Fig. 2), is hereby designated the lectotype. The smallest of the paralectotypes, BMNH 1946.1.21.27, was illustrated by Kofron (1982: fig. 1), and the lectotype and female paralectotype (BMNH 1946.1.21.28) are illustrated herein (Figs. 2, 3). A fine artistic rendering of the head and anterior body of the female paralectotype (the largest specimen) was given in the original description (Boulenger, 1898: pl. XII, fig. 2).

The lectotype is an adult male in good

Table 1. Comparisons of size and standard characters in *Dipsas ellipsifera*, *D. elegans*, and *D. oreas*. For head scales, each side of the head was scored separately because individual specimens were frequently bilaterally asymmetrical. Two data summaries for *D. oreas* data are presented (columns 3 and 4): Ecuadorian specimens only (for direct comparison with *D. elegans* and *D. ellipsifera*; see text) and the total sample (Ecuadorian + Peruvian specimens of *D. oreas*; see Table 3 for additional breakdown of data for *D. oreas*). $N$ = Number of specimens or observations; SVL = snout to vent length.

| | | | *Dipsas oreas* | |
|---|---|---|---|---|
| | *Dipsas ellipsifera* | *Dipsas elegans* | Ecuador | Total sample |
| Total length (SVL) (mm) | | | | |
| Largest male | 566 (417) | 683+ (515+) | 691 (509) | 758 (547) |
| Largest female | 630 (488) | 782 (587) | 827 (626)[1] | 827 (626) |
| Tail length/total length | | | | |
| Male | 0.24–0.27<br>0.25 ± 0.01 ($N$ = 7) | 0.26–0.28<br>0.27 ± 0.009 ($N$ = 6) | 0.25–0.26<br>0.26 ± 0.01 ($N$ = 8) | 0.25–0.28<br>0.26 ± 0.008 ($N$ = 18) |
| Female | 0.21–0.22<br>0.215 ± 0.007 ($N$ = 2) | 0.22–0.26<br>0.24 ± 0.018 ($N$ = 5) | 0.23–0.24<br>0.24 ± 0.005 ($N$ = 8) | 0.21–0.24<br>0.24 ± 0.009 ($N$ = 14) |
| Maxillary teeth | 15 ($N$ = 1)<br>16 ($N$ = 2)<br>17 ($N$ = 2)<br>18 ($N$ = 1) | 17 ($N$ = 6)<br>18 ($N$ = 3)<br>19 ($N$ = 2)<br>21 ($N$ = 1) | 12 ($N$ = 4)<br>13 ($N$ = 7)<br>14 ($N$ = 2) | 12 ($N$ = 6)<br>13 ($N$ = 8)<br>14 ($N$ = 9) |
| Dorsal scales | 15-15-15 ($N$ = 8)<br>16-15-15 ($N$ = 1) | 15-15-15 ($N$ = 9)<br>16-15-15 ($N$ = 1)<br>15-15-13 ($N$ = 3)<br>15-17-16 ($N$ = 1) | 15-15-15 ($N$ = 15)<br>16-15-15 ($N$ = 1)<br>15-15-13 ($N$ = 1) | 15-15-15 ($N$ = 35)<br>16-15-15 ($N$ = 1)<br>15-15-13 ($N$ = 1)<br>15-17-15 ($N$ = 1) |
| Ventrals | | | | |
| Male | 153–164<br>157.4 ± 3.51 ($N$ = 7) | 177–189<br>181.5 ± 4.44 ($N$ = 8) | 173–184<br>178.6 ± 3.38 ($N$ = 8) | 167–184<br>175.7 ± 4.95 ($N$ = 21) |
| Female | 157–158<br>157.5 ± 0.71 ($N$ = 2) | 166–178<br>172.4 ± 5.13 ($N$ = 5) | 171–181<br>178.2 ± 3.12 ($N$ = 10) | 167–181<br>175.8 ± 4.58 ($N$ = 16) |
| Subcaudals | | | | |
| Male | 72–78<br>74.8 ± 2.03 ($N$ = 7) | 94–105<br>98.0 ± 4.19 ($N$ = 6) | 82–87<br>85.3 ± 2.06 ($N$ = 7) | 82–91<br>86.6 ± 2.43 ($N$ = 19) |
| Female | 62–63<br>62.5 ± 0.71 ($N$ = 2) | 68–88<br>80.0 ± 7.62 ($N$ = 5) | 74–83<br>76.4 ± 3.20 ($N$ = 8) | 70–83<br>76.1 ± 3.27 ($N$ = 14) |
| Total segmental counts | | | | |
| Male | 229–242 ($N$ = 7) | 272–294 ($N$ = 6) | 258–271 ($N$ = 7) | 251–271 ($N$ = 22) |
| Female | 220 ($N$ = 2) | 237–260 ($N$ = 5) | 245–263 ($N$ = 8) | 241–263 ($N$ = 14) |
| Anal scale | Single | Single | Single | Single |

TABLE 1. CONTINUED.

| | *Dipsas ellipsifera* | *Dipsas elegans* | *Dipsas oreas* | |
|---|---|---|---|---|
| | | | Ecuador | Total sample |
| Loreal pattern | 3 ($N$ = 16) | 3 ($N$ = 24) | 1 ($N$ = 12) | 1 ($N$ = 12) |
| | 4 ($N$ = 2) | 4 ($N$ = 2) | 2 ($N$ = 18) | 2 ($N$ = 44) |
| | | | 5 ($N$ = 4) | 5 ($N$ = 5) |
| | | | | 6 ($N$ = 13) |
| Preoculars | 0 ($N$ = 2) | 0 ($N$ = 2) | 0 ($N$ = 18) | 0 ($N$ = 44) |
| | 1 ($N$ = 17) | 1 ($N$ = 24) | 1 ($N$ = 16) | 1 ($N$ = 30) |
| Postoculars | 2 ($N$ = 18) | 1 ($N$ = 2) | 2 ($N$ = 19) | 1 ($N$ = 4) |
| | | 2 ($N$ = 23) | 3 ($N$ = 13) | 2 ($N$ = 39) |
| | | | 4 ($N$ = 2) | 3 ($N$ = 31) |
| | | | | 4 ($N$ = 2) |
| Primary temporals | 2 ($N$ = 18) | 1 ($N$ = 4) | 1 ($N$ = 9) | 1 ($N$ = 13) |
| | | 2 ($N$ = 20) | 2 ($N$ = 21) | 2 ($N$ = 42) |
| | | 3 ($N$ = 1) | 3 ($N$ = 4) | 3 ($N$ = 18) |
| | | | | 4 ($N$ = 1) |
| Secondary temporals | 2 ($N$ = 3) | 2 ($N$ = 4) | 2 ($N$ = 3) | 2 ($N$ = 4) |
| | 3 ($N$ = 15) | 3 ($N$ = 20) | 3 ($N$ = 24) | 3 ($N$ = 47) |
| | | 4 ($N$ = 1) | 4 ($N$ = 6) | 4 ($N$ = 22) |
| Supralabials (touching eye) | 6 (3–4) $N$ = 1 | 6 (3–4) $N$ = 2 | 7 (3–5) $N$ = 7 | 6 (2–4) $N$ = 1 |
| | 6 (4) $N$ = 1 | 6 (4–5) $N$ = 1 | 7 (4–5) $N$ = 6 | 6 (3–4) $N$ = 2 |
| | 7 (3–5) $N$ = 1 | 7 (3–5) $N$ = 1 | 8 (3–5) $N$ = 4 | 7 (3–4) $N$ = 1 |
| | 7 (4–5) $N$ = 10 | 7 (4–5) $N$ = 10 | 8 (4–5) $N$ = 1 | 7 (3–5) $N$ = 16 |
| | 8 (4–5) $N$ = 3 | 8 (3–5) $N$ = 1 | 8 (4–6) $N$ = 13 | 7 (4–5) $N$ = 18 |
| | 8 (4–6) $N$ = 1 | 8 (4–5) $N$ = 3 | 9 (4–6) $N$ = 1 | 8 (3–4) $N$ = 1 |
| | 8 (5–6) $N$ = 1 | 8 (4–6) $N$ = 4 | 9 (4–7) $N$ = 1 | 8 (3–5) $N$ = 6 |
| | | 8 (5–6) $N$ = 1 | | 8 (4–5) $N$ = 10 |
| | | 9 (4–6) $N$ = 1 | | 8 (4–6) $N$ = 16 |
| | | 9 (4–7) $N$ = 1 | | 9 (4–6) $N$ = 1 |
| | | | | 9 (4–7) $N$ = 1 |
| Intralabials | 8 ($N$ = 1) | 8 ($N$ = 1) | 9 ($N$ = 1) | 9 ($N$ = 1) |
| | 9 ($N$ = 1) | 9 ($N$ = 3) | 10 ($N$ = 5) | 10 ($N$ = 7) |
| | 10 ($N$ = 12) | 10 ($N$ = 10) | 11 ($N$ = 15) | 11 ($N$ = 20) |
| | 11 ($N$ = 4) | 11 ($N$ = 6) | 12 ($N$ = 12) | 12 ($N$ = 31) |
| | | 12 ($N$ = 5) | 13 ($N$ = 2) | 13 ($N$ = 16) |
| Number of dorsal bands/ blotches on body | 30–39<br>34.2 ± 3.56 ($N$ = 9) | 26–46<br>34.3 ± 5.81 ($N$ = 13) | 19–30<br>24.9 ± 2.96 ($N$ = 17) | 17–30<br>22.6 ± 3.38 ($N$ = 34) |

[a] The largest female of *D. oreas* is the holotype of *Leptognathus andrei* Sauvage, from measurements reported by Kofron (1982: 49) (not examined for this study).

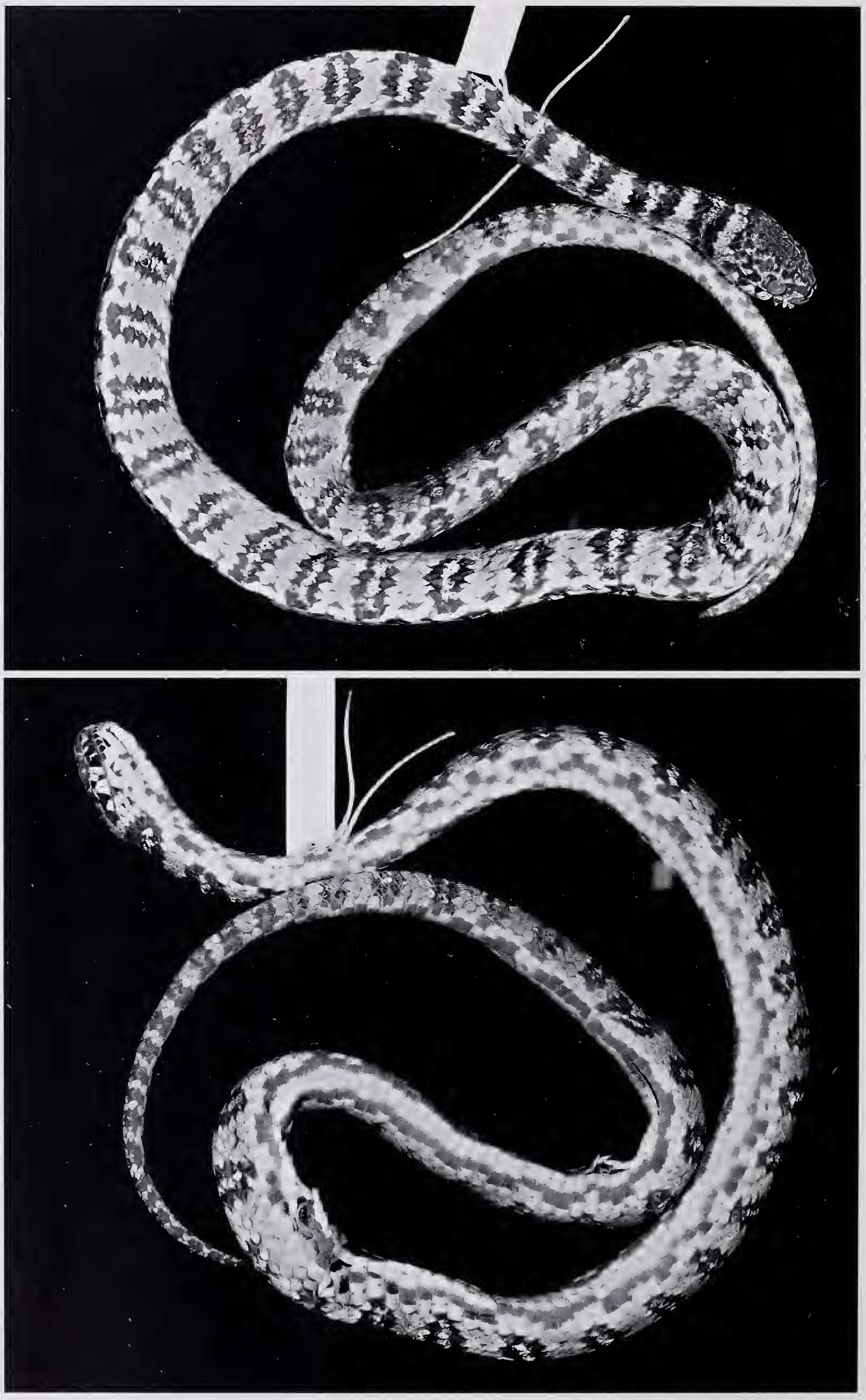

Figure 2. *Dipsas ellipsifera* (Boulenger). Male lectotype in dorsal and ventral views (BMNH 1946.1.21.26; 349 mm SVL).

TABLE 2. STANDARD CHARACTERS OF THE LECTOTYPE AND PARALECTOTYPES OF *DIPSAS ELLIPSIFERA*. BILATERAL COUNTS ARE SEPARATED BY A SOLIDUS (LEFT/RIGHT). SVL = SNOUT TO VENT LENGTH.

| | Lectotype BMNH 1946.1.21.26 male | Paralectotype BMNH 1946.1.21.27 male | Paralectotype BMNH 1946.1.21.28 female | Paralectotype BMNH 1946.1.21.29 male |
|---|---|---|---|---|
| Total length (SVL) (mm) | 465 (349) | 265 (202) | 630 (488) | 336 (254) |
| Tail length/total length | 0.27 | 0.24 | 0.22 | 0.24 |
| Maxillary teeth | 18 | — | 16 | — |
| Dorsal scales | 16-15-15 | 15-15-15 | 15-15-15 | 15-15-15 |
| Ventrals (and preventrals) | 158 (2) | 159 (3) | 157 (1) | 156 (2) |
| Subcaudals | 73 | 75 | 63 | 74 |
| Total segmental counts | 231 | 234 | 220 | 230 |
| Anal scale | Single | Single | Single | Single |
| Loreal pattern | 3/3 | 3/3 | 3/3 | 4/3 |
| Preoculars | 1/1 | 1/1 | 1/1 | 0/1 |
| Postoculars | 2/2 | 2/2 | 2/2 | 2/2 |
| Primary temporals | 2/2 | 2/2 | 2/2 | 2/3 |
| Secondary temporals | 3/3 | 3/3 | 3/3 | 2/2 |
| Tertiary temporals | 4/4 | 3/4 | 3/4 | 3/3 |
| Supralabials (touching eye) | 7 (4–5)/7 (4–5) | 8 (4–5)/7 (4–5) | 7 (4–5)/8 (5–6) | 7 (4–5)/6 (4) |
| Infralabials | 10/10 | 11/11 | 10/10 | 11/10 |
| Number of infralabials in contact behind mental | 1 pair | 2 pairs | 1 pair | 1 pair |
| Number of bands or blotches on body | 39 | 38 | 31 | 30 |

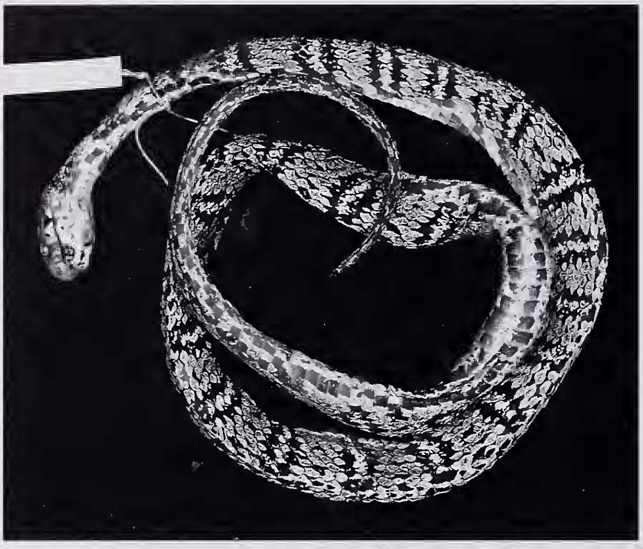

Figure 3. Female paralectotype of *Dipsas ellipsifera* (BMNH 1946.1.21.28; 488 mm SVL).

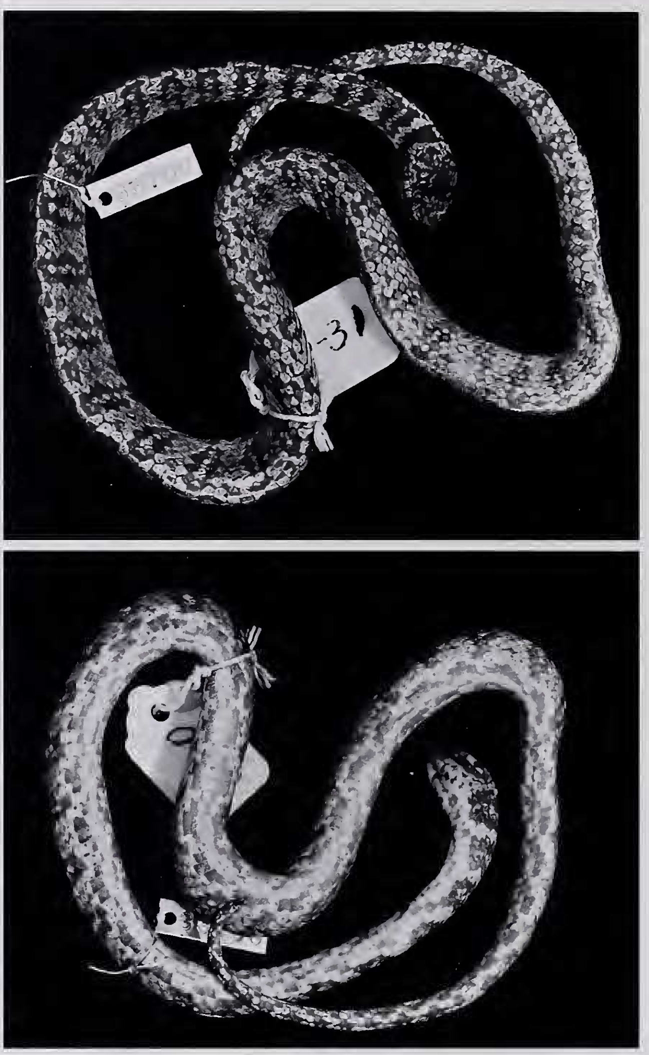

Figure 4. *Dipsas ellipsifera* (Boulenger). Dorsal and ventral views of UMMZ 83700, an adult from Pimampiro, Ecuador (349 mm SVL).

condition and has a color pattern and general characteristics typical of all specimens of *Dipsas ellipsifera* examined. In addition to details reported for the lectotype in Table 2, it is worth noting that the dorsal formula of 16-15-15 is a variation occasionally observed within *Dipsas*. The lectotype has a relatively longer tail (27% of total length) than other specimens of *D. ellipsifera* examined. Comments concerning the color patterns of the syntypes are given in the section on coloration below.

## Diagnosis

*Dipsas ellipsifera* is characterized by a low number of ventrals (153–164 in seven males, 157–158 in two females) and subcaudals (72–78 in males, 62–63 in females). Its color pattern consists of 30 to 40 markings, each of which has a characteristic composition. Each marking typically appears as a closely spaced pair of black bars or bands with a central whitish area (Figs. 2–5, 7); edges of the markings are more or less vertical. The markings may be continuous across the vertebral region, forming complete bands, or contralateral markings may fail to meet in the vertebral region, forming a series of lateral bars. The anterior five or six markings are broader than more posterior ones and are equivalent to, or broader than, the light interspaces. Posterior markings are narrower than the interspaces.

*Dipsas ellipsifera* differs from all other species of *Dipsas* in western Ecuador by its low number of ventrals and subcaudals and additionally differs from all species except *D. elegans* in color pattern (see Table 1 and the key accompanying this report). *Dipsas andiana, D. gracilis,* and *D. temporalis* all have >180 ventrals, >80 subcaudals, and patterns that do not involve narrow bands or bars with light centers. *Dipsas oreas* has >165 ventrals, >65 subcaudals, and a different color pattern (see below). Additional commentary is warranted concerning the most similar spe-

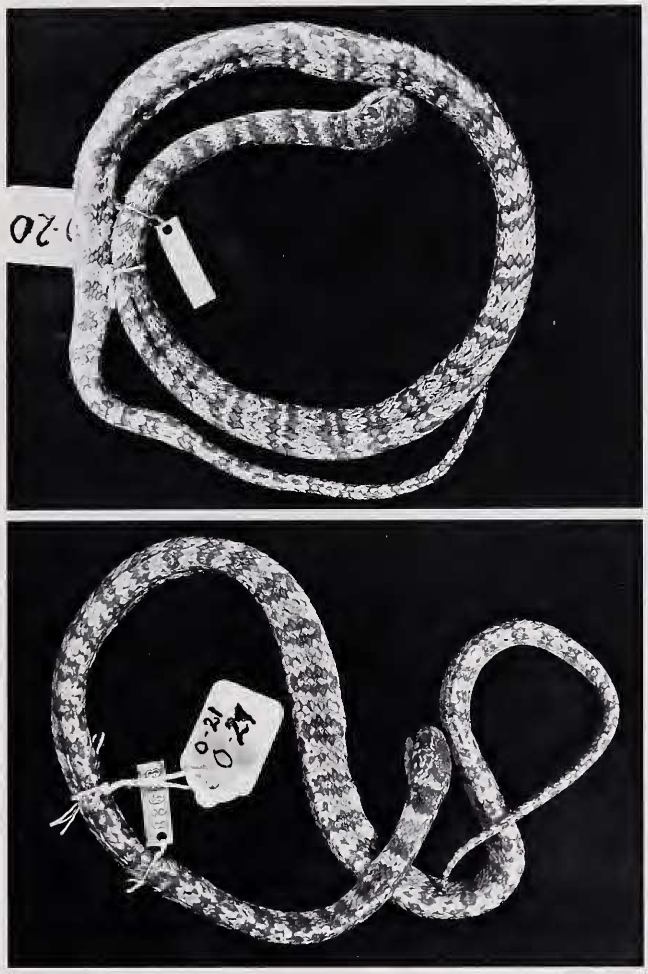

Figure 5. *Dipsas ellipsifera* (Boulenger). Dorsal views of representative adult specimens from Pimampiro, Ecuador. **Top:** UMMZ 83697 (386 mm SVL). **Bottom:** UMMZ 83698 (357 mm SVL).

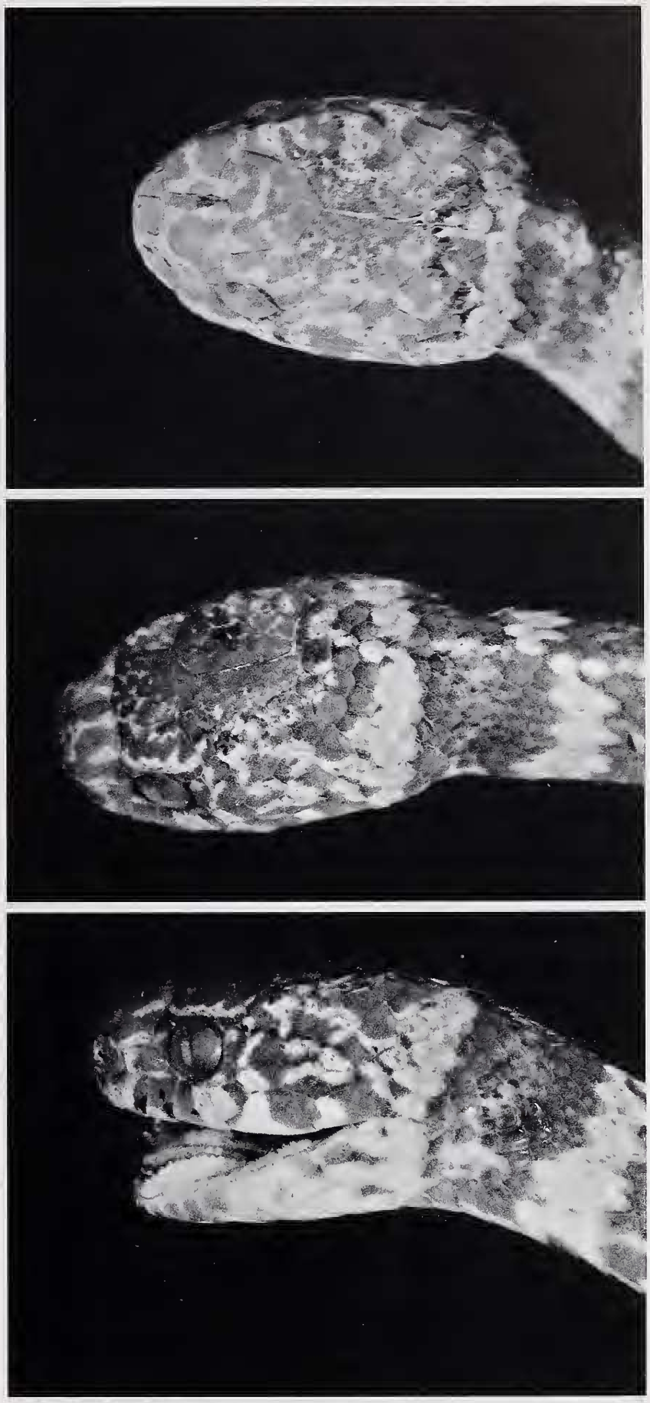

Figure 6. Head patterns of *Dipsas ellipsifera* (Boulenger). **Top:** UMMZ 83697. **Middle and bottom:** UMMZ 83698 (dorsal and lateral). Both specimens from Pimampiro, Ecuador.

cies, *D. elegans,* in view of their similar color patterns and the previous confusion of the two species (e.g., Kofron, 1982; Peters, 1960a). The distinctions are most clearly seen by separately comparing the sexes.

*Dipsas ellipsifera* differs from *D. elegans* (see Table 1) in having fewer ventrals (*D. elegans*: 177–189 in males; 166–178 in females) and subcaudals (*D. elegans*: 94–105 in males; 68–88 in females), a smaller relative eye size, and a differently shaped head (Figs. 6, 10). The head of adult *D. ellipsifera* is small relative to body size and has rounded canthal and temporal regions, whereas the head of adult *D. elegans* is larger, blocky, and has angular canthal and temporal regions. On the basis of a few observations for *D. ellipsifera,* it seems that small juveniles of this species (≤210 mm snout–vent length [SVL]) already manifest the adult color pattern (e.g., Fig. 7), whereas small juveniles of *D. elegans* (Figs. 11, 12) have solid dorsal bands that only develop light centers somewhat later

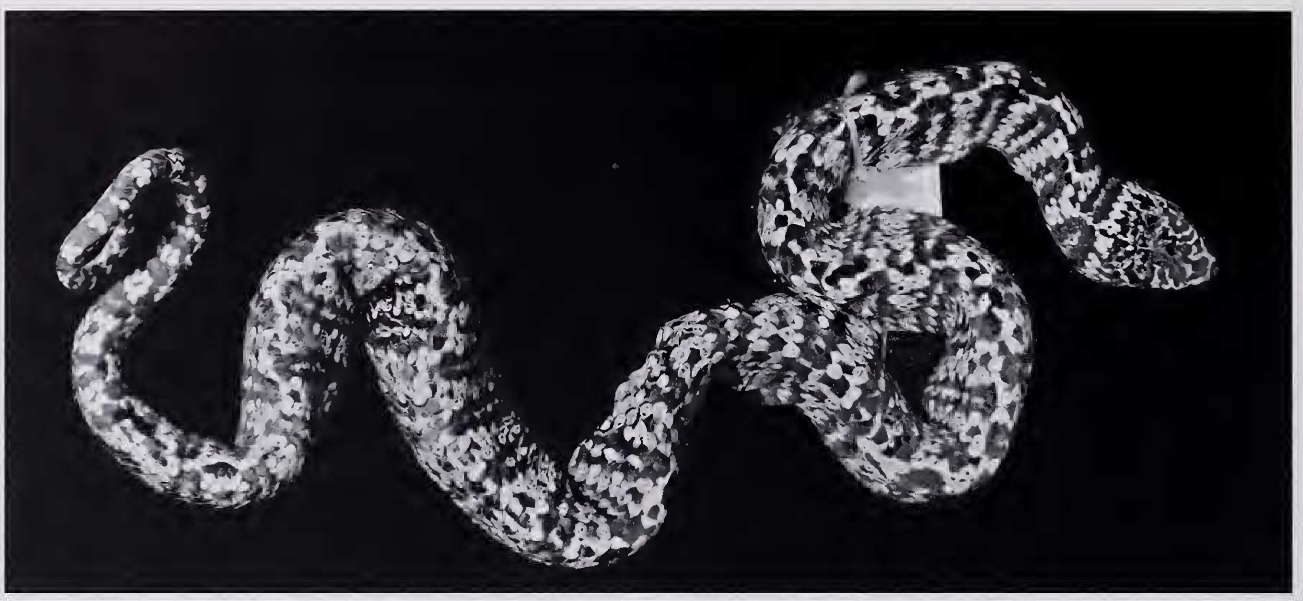

Figure 7. *Dipsas ellipsifera* (Boulenger). A small juvenile from the type locality, Ibarra, Ecuador (MCZ 8431, 210 mm SVL).

(see color descriptions in the species accounts).

## Description

Characteristics of *Dipsas ellipsifera* are summarized in Table 1.

*Size, Scutellation and Description.* The largest specimen is a female 630 mm total length, 488 mm SVL. Largest male 566 mm total length, 417 mm SVL. Tail 24–27% of total length in seven males, 21–22% in two females. Body strongly compressed. Dorsal scales in 15-15-15 rows (rarely 16-15-15). Vertebral scale row approximately 2–2¼× the width of paravertebral rows. Ventrals 153–164 (averaging 157) in seven males; 157–158 (averaging 157.5) in two females. Males and females apparently not sexually dimorphic in ventral number. One to three preventrals precede the ventral series (see Myers, 2003, for discussion). Subcaudals 72–78 (averaging 75) in seven males, 62–63 (averaging 62.5) in two females. Total segmental counts 229–242 in seven males, 220 in two females. An elongate rectangular loreal and a small preocular border the anterior edge of the eye in most specimens; preocular superior to loreal (Fig. 1: loreal pattern 3). Preocular sometimes fused with prefrontal, which then borders the eye above the loreal (Fig. 1: loreal pattern 4). Head scales highly variable (Table 1): postoculars 2, primary temporals 2, secondary temporals usually 3 (sometimes 2). Supralabials 6–8 with varying combinations bordering the eye (Table 1); the most common pattern is 7 supralabials with 4–5 bordering the eye. Infralabials usually 10 (range 8–11). Either one pair ($N = 5$) or two pairs ($N = 3$) of infralabials in contact behind the mental. Two pairs of squarish chin shields followed by one or two pairs of offset gular scales that are wider than long. Maxillary teeth 15–18 ($N = 6$).

*Color in Life.* Unknown.

*Color and Pattern in Preservative.* In addition to illustrations herein, other illustrations of *Dipsas ellipsifera* include a detail of the midbody pattern of an adult male (Peters, 1960a: pl. IVa; UMMZ 83699, 417 mm SVL); dorsal and ventral views of a juvenile male paralectotype, BMNH 1946.1.21.27 (Kofron, 1982: fig. 1; 138 mm SVL); and an artistic rendering of BMNH 1946.1.21.28 in the original description (Boulenger, 1898: pl. XII, fig. 2).

The dorsal ground color of adults is dull pale brown or grayish with 30–39 paired dark brown bands or bars on the body (Figs. 2–5, 7). Each band or bar consists of a pair of bold, blackish, more or less vertical markings separated by a narrow whitish strip. In some specimens the contralateral markings meet in the vertebral region, forming more or less complete bands, although the vertebral region tends to be invested with dark pigment so that the pale central regions of the markings are interrupted. In others (e.g., MCZ 8431; Fig. 7), contralateral markings fail to meet middorsally, forming lateral bars with pale centers that are closed off on their dorsal edges by black pigment. The markings have vertical edges and extend ventrally to the first scale row or the outer edge of the ventrals. Contralateral markings are frequently offset virtually the entire length of the body (e.g., Fig. 7) or on the posterior body only (most specimens). The markings (i.e., each black–white–black triplet) are 5–6 scale rows in width anteriorly but narrow to about 3 rows by midbody. Interspaces anteriorly are narrower than the bands or bars (approximately 3 scale rows), whereas they are wider than the markings posteriorly (5–6 scale rows). The venter is dull grayish brown with a dense covering of dark brown squarish markings that tend to be concentrated toward the outer edges of the ventrals, sometimes forming longitudinal arrays (Figs. 2–4).

The top and sides of the head are heavily marked with irregular dark markings on a pale brown ground color (Fig. 6). The markings are so extensive in some specimens that most of the top of the head is a solid dark brown, with just occasional light areas of the ground color showing through as fine reticulations or vermiform marks. Upper and lower labials are pale brown with dark brown spotting, but the dark stippling often is not especially concentrated along suture lines as in many species of snakes.

Two small juveniles (MCZ 8431, 210 mm SVL; BMNH 1946.1.21.27, 138 mm SVL) have patterns identical to those of adults, but more contrasting (Fig. 7; Kofron, 1982: fig. 1). The ground color is grayish white, and the dark markings are dark chocolate brown to blackish. The dorsal markings have pale centers and appear as blackish vertical bars (or narrow ellipses) enclosing whitish centers. Interspaces between the markings are whitish, but individual scales are speckled with tiny irregular dark brown flecks. The top of the head of MCZ 8431 is whitish with heavy reticulations and irregular spots so that much of the top and sides of the head are dark. The gular regions and venter are whitish with a pattern of bold irregular spots and blotches; on the venter these tend to form bold longitudinal streaks. If these two specimens are representative of very small individuals of *Dipsas ellipsifera*, this species appears already to have the adult color pattern even as small juveniles, a contrast with the developmental pattern in *D. elegans* and *D. oreas* (see the following species accounts for discussion). In the last two species, smallest juveniles have solid bands that develop pale centers during early juvenile ontogeny, thus acquiring the adult patterns sometime after hatching.

### Hemipenis

The following description is based on the inverted organ of UMMZ 83697 examined in situ. The organ had previously been slit along its medial edge and the retractor muscle had been cut distal to its point of division.

Total length of the organ is 18 mm and it is slightly bilobed distally. The retractor muscle is divided proximally for 4 mm. The sulcus spermaticus (in the lateral wall of the organ) divides 9 mm from the base of the organ within the capitulum; the tips of its branches end approximately 1 mm short of the distal tips of the lobes. The basal region of the organ is sparsely ornamented with minute spines. The midsection has a battery of enlarged hooked spines encircling the organ just proximal to the capitulum; the battery is about 3 spines across around the entire organ. The capitulum is set off by a distinct overhang and is completely ornamented distally with well-developed papillate calyces. However, the proximal papillae, especially those adjacent to the fork of the sulcus spermaticus and those fringing the overhang, have mineralized tips. A very large (8 mm long) nude pocket extends from the base of the organ to the battery of spines; its distal end is nestled within the proximal spines of the battery. The pocket is on the dorsal surface of the inverted organ (=the lateral surface of the everted organ relative to the sulcus spermaticus). The pocket has a large lobe on its absulcate edge and a smaller lobe on its sulcate edge; these lobes also bear minute scattered spines. The asulcate side of the organ (medial side of the inverted organ) bears 3 enlarged spines in a transverse row, which are separated by a gap (ornamented with minute spines) from the battery of spines on the midsection.

The hemipenis of *Dipsas ellipsifera* is similar in many details to hemipenes of other snakes of the tribe Dipsadini that have been described (review in Cadle and Myers, 2003: 14–15). Features common to hemipenes of the Dipsadini include well-developed papillate calyces on the capitulum, an encircling battery of enlarged spines on the midsection, a relatively unornamented base, and a very large nude pocket proximally on either the asulcate or lateral surface of the organ. The nude pocket in *D. ellipsifera* is exceptionally long, 44% of the length of the organ. In other species examined by Cadle and Myers (2003: 15) the pocket was approximately 33% of the length of the organ. However, observations in Cadle and Myers (2003) were based on everted organs and it is not possible to know the relative proportions of the nude pocket in the everted hemipenis of *D. ellipsifera* because hemipenial tissue expands differentially upon eversion (see Myers and Cadle, 2003). The proximally divided retractor muscle in *D. ellipsifera* suggests that its everted hemipenis may be somewhat more bilobed than everted hemipenes of either *D. elegans* or *D. oreas* described later herein. The degree of bilobation apparently varies among species of *Dipsas* (Cadle and Myers, 2003: 14–15).

## Distribution and Natural History

*Dipsas ellipsifera* is known only from the valley of the Río Mira in extreme northwestern Ecuador (Fig. 8). All reported specimens are from Imbabura Province; the Río Mira divides Imbabura from Carchi Province, and the species may also occur in the latter province. Elevations for the two localities for which specimens were examined in this study are 2,000 and 2,211 m, but Orcés and Almendáriz (1987) reported an elevational range of 572–2,600 m for this species (see *Specimens Examined and Locality Records*). Several specimens collected by Philip Hershkovitz (UMMZ 83697–700) were obtained in June and August, but most specimens are not accompanied by specific collection dates.

The type locality of *Dipsas ellipsifera*, Ibarra, lies at 2,211 m elevation in a dry rain shadow valley of the western Andes. Rosenberg (quoted in Hartert, 1898) described the vicinity of Ibarra at the time the syntypes were collected as "... open, and for the most part cultivated," seemingly quite different from a nearby locality at a lower elevation to the west, Paramba (=Hacienda Paramba; Paynter, 1993), which Rosenberg described as "densely forested." Orcés and Almendáriz (1987: 138) stated the following concerning localities for *D. ellipsifera*: "... [the localities] are found in the subtropical and temperate zones. The region in question is for the most part semiarid with shrubby vegetation; in a few cases epiphytic and parasitic plants are present. The temperature varies from 18° to 22° C and the precipitation from 500 to 1,000 mm." Lita, the most western locality and the lowest elevation (572 m) from which *D. ellipsifera* has been recorded (Orcés and Almendáriz, 1987), lies in the region of very humid lowland rain forest characteristic of northwestern Ecuador.

Because Peters (1960a) confused some

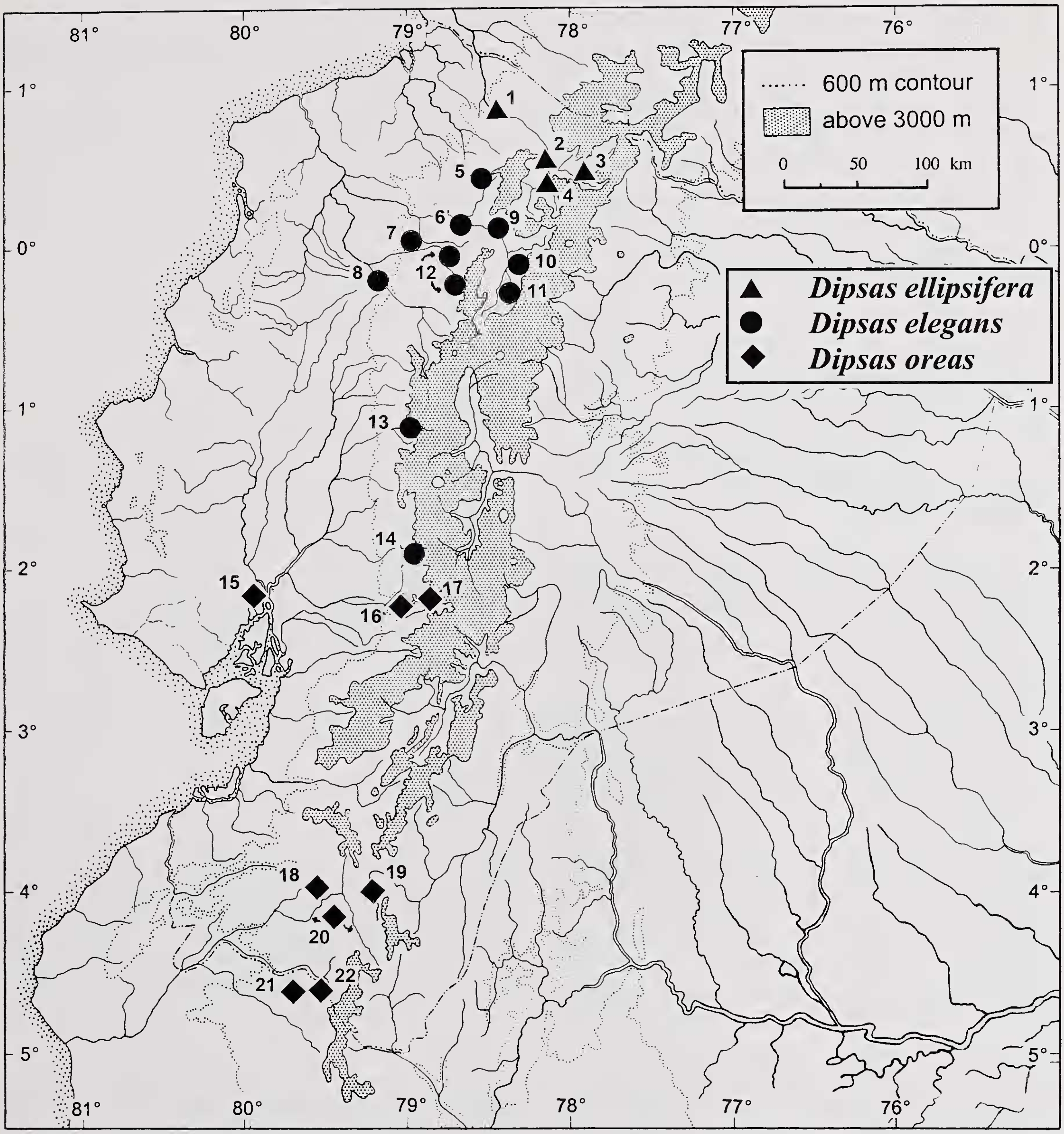

Figure 8. Locality records for *Dipsas ellipsifera, D. elegans,* and *D. oreas* in western Ecuador and extreme northern Peru. See Figure 23 for other known Peruvian localities for *D. oreas.* A few symbols for *D. elegans* and *D. oreas* represent pairs of contiguous localities; otherwise, all localities considered reliable are plotted (see text and list of specimens and localities). Numbered localities. *Dipsas ellipsifera*: **(1)** Lita (Orcés and Almendáriz, 1987); **(2)** Chachimbiro (Orcés and Almendáriz, 1987); **(3)** Pimampiro; **(4)** Ibarra (type locality). *Dipsas elegans*: **(5)** Peñaherrera; **(6)** Nanegal Grande and Pacto; **(7)** Río Saloya; **(8)** Santo Domingo de los Colorados; **(9)** Perucho (Orcés and Almendáriz, 1987); **(10)** El Quinché (Orcés and Almendáriz, 1987); **(11)** Cumbayá and Tumbaco (Orcés and Almendáriz, 1987); **(12)** Mindo (north) and Chiriboga (south; Orcés and Almendáriz, 1987); **(13)** Corazón; **(14)** Pallatanga. *Dipsas oreas*: **(15)** Guayaquil; **(16)** Huigra/Río Chiguancay and Río Chanchan valley; **(17)** Alausí (Despax, 1911); **(18)** Velacruz; **(19)** Loja; **(20)** Río Catamayo; **(21)** Ayabaca (Peru); **(22)** Cerro Aypate (Peru).

specimens of *Dipsas elegans* with *D. ellipsifera* (see above nomenclatural history), several specimens and associated localities he listed for *D. ellipsifera* are known or probable errors. UMMZ 98073 (Peñaherrera-Intag) is here referred to *D. elegans.* Three specimens that Peters (1960a) cited from the Escuela Politécnica Nacional (EPN, Quito), EPN 719 ("camino a Mindo") and EPN 717–718 ("El Corazón"), are probably equivalent to specimens referred herein to *D. elegans,* which Peters obtained from Orcés and later catalogued at the USNM (see *Specimens Examined and Locality Records* and footnote 9).

## ***Dipsas elegans* (Boulenger)**
## **Figures 8–13**

*Leptognathus mikanii,* part: Günther, 1885–1902: 141. Boulenger, 1896: 454: variant C ("*L. oreas,* Cope"), specimens *c, d* from "W. Ecuador" (=BMNH 60.6.16.73) and "Pallatanga, Ecuador" (=BMNH 80.12.5.267; Fig. 13), respectively [misidentifications].

*Leptognathus elegans* Boulenger, 1896: 452. Holotype BMNH 1946.1.21.77 (original number 71.2.7.36). Type locality unknown, "Tehuantepec" [Mexico], in error. The type locality was discussed by Kofron (1982), who concluded that the specimen must have come from Ecuador (see above discussion). Orcés and Almendáriz (1987: 139) unjustifiably inferred that Perucho (Pichincha Province) "could be considered the type locality." The holotype was illustrated by Kofron (1982: Fig. 1).

*Sibynomorphus elegans*: Amaral, 1926: 9. Amaral, 1929a: 29. Amaral, "1929"b [1930]: 197.

*Leptognathus maxillaris* Werner: Amaral, 1929a: 29, "1929"b [1930]: 197.[4] Kofron (1982: 46) examined the holotype of *L. maxillaris* and stated that it was "badly faded and cannot be allocated to any known form at this time . . . [but] possibly the same taxon as *L. elegans.*"

*Dipsas elegans*: Parker, 1926: 206. Smith and Taylor, 1945: 51. Peters, 1960a: 86. Peters, 1965: 3. Miyata, 1982: 16.

*Dipsas oreas,* part: Peters (1960a: 94) based on BMNH 1940.2.20.32 from "Río Saloya, Ecuador" [misidentification]. Identification of the same specimen (as "*Dipsas oreas oreas*") also accepted by Orcés and Almendáriz (1987: 140).

*Dipsas ellipsifera*: Kofron, 1982:46.

*Dipsas oreas elegans*: Orcés and Almendáriz, 1987: 138. Pérez-Santos and Moreno, 1991: 154.

### Notes on the Holotype

Photographs of the holotype of *Leptognathus elegans* (BMNH 1946.1.21.77) were presented by Kofron (1982: fig. 1) and accurate artistic renderings were given in the original description (Boulenger, 1896: pl. XVIII, fig. 3). The specimen has a color pattern typical of other specimens of *Dipsas elegans* with SVL greater than about 200 mm (see discussion below on ontogeny of color pattern and Figs. 11 and 12 for examples). Its presumed provenance from western Ecuador was discussed previously herein.

The holotype is a subadult male with the following characteristics (differences from those reported by Kofron, 1982: 46–47 reported in parentheses): Total length, 301 mm. Tail length, 78 mm. SVL, 223 mm. Tail as a proportion of total length, 26%. Dorsal scales in 15-15-15 rows. Vertebral row about 2× the width of paravertebral rows. Ventrals, 182 + 1 preventral (183). Subcaudals, 95. Anal scale single. Preoculars, 1/1, situated superior to an elongate loreal, which touches the eye. Postoculars, 2/2. Temporals, 2 + 3 + 3/2 + 2 + 3. Loreal pattern 3 (small preocular superior to an elongate loreal). Supralabials, 8/8 with 4–5 touching the eye on each side. Infralabials, 10/10; one pair of infralabials meeting behind the mental scale. Two pairs of subequal squarish chin shields followed by two pairs of offset gular scales. Maxillary teeth 17 (18) (my count taken on the left side; not stated by Kofron).

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[4] Laurent (1949) and Smith and Taylor (1945) did not wholeheartedly accept Amaral's synonymy. However, they questioned the synonymy primarily because the holotype of *Leptognathus maxillaris* differs from *Dipsas elegans* by characters that are now known to be highly variable within species of *Dipsas* (e.g., labial counts, patterns of scales in the temporal region, and number of infralabials in contact behind the mental). Peters (1960a: 49) pointed out these issues but thought the problem needed additional study (he maintained *maxillaris* distinct from *elegans*).

The holotype of *Leptognathus maxillaris* was said to be from "Tabasco, Mexico," and Amaral (1929a,"1929"b [1930]) considered it a synonym of *D. elegans,* in part, because the type locality of *L. elegans* was understood (erroneously) to be "Tehuantepec" [Mexico]. Werner (1909: 279–280) reported the following characteristics (among others) for the holotype of *L. maxillaris*: 180 ventrals, 84 subcaudals, 6 supralabials (3 + 4 touching the eye), 40 "coffee brown" bands on the body, total length 335 mm, tail length 70 mm. Laurent (1949) stated that the holotype was a female. These characteristics and others reported by Laurent (1949) and Werner (1909) are consistent with characteristics of female *D. elegans,* although the relative tail length (21% of total length) is slightly lower than in specimens I examined (Table 1). As with other poorly illustrated type descriptions of *Dipsas* spp., reexamination of the holotype of *D. maxillaris* will ultimately be necessary to confirm its identity, although this could be problematic if, as reported by Kofron (1982), no elements of pattern remain on the specimen.

Dorsal bands or blotches on body 40, each band consisting of a pair of bold, blackish, vertical bars with crenulated edges, between which is a narrow white bar (thus giving the appearance of dark bands with pale central portions). Anterior bands are 3–4 dorsal rows wide, narrowing to 3 rows by midbody and 2 rows posteriorly. Central white portion of bands 1 scale or less in width. The first five bands are not offset but all remaining bands are slightly to greatly offset, failing to join middorsally; the offset increases posteriorly. The dorsal bands extend down to outer edges of ventrals. The venter has bold squarish blotches that tend to align longitudinally into irregular streaks spanning several ventral scales. The top of the head is dark brown, concentrated more centrally (more white pigment on prefrontals, internasals, supraoculars, and peripheral parietal region). Many white fine reticulations and irregular marks are on the top of the head.

In addition to these characters, Kofron (1982) reported additional details, such as head measurements, head scale proportions, color pattern details (herein incorporated into the general description), and dentary teeth (22).

## Diagnosis

*Dipsas elegans* is characterized by a moderate number of ventrals (177–189 in eight males, 166–178 in five females) and subcaudals (94–105 in males, 68–88 in females). Its color pattern consists of 26 to 46 narrow dark dorsal bands which, except in small juveniles (see below), have light centers (Figs. 9, 11–13). The bands have more or less vertical edges. The anterior five or six bands are broader than more posterior bands and are equivalent to, or broader than, the light interspaces. Posterior bands are narrower than the interspaces.

*Dipsas elegans* differs from other species in western Ecuador except *D. ellipsifera* by its distinctive color pattern (each band consisting of a pair of dark edges enclosing a contrasting pale center). *Dipsas gracilis* and *D. temporalis* have very broad black bands without pale centers. *Dipsas andiana* has a distinctive U- or V-shaped marking on the top of the head and a pattern of lateral blotches that lack pale centers (Cadle and Myers, 2003). The two species most often confused with *D. elegans* are *D. ellipsifera* and *D. oreas*. *Dipsas ellipsifera* differs from *D. elegans* in having fewer ventrals and subcaudals and a different head shape (see above diagnosis for *D. ellipsifera*).

Orcés and Almendáriz (1987), following a suggestion by Kofron (1982: 50), considered *Dipsas elegans* only subspecifically distinct from *D. oreas*. However, Kofron's suggestion was based only on the similarity in segmental counts in the two species, which is common among species of *Dipsas*. Several characteristics distinguish these species when data are analyzed separately for males and females to account for sexual dimorphism.

*Dipsas elegans* and *D. oreas* have quite distinct color patterns and I am unaware of intermediate specimens (compare Figs. 9, 13 with Figs. 14–19 for general dorsal patterns; Fig. 10 with Figs. 20–22 for head patterns). A specimen from the southernmost known locality for *D. elegans* (Fig. 13) has a color pattern typical of all specimens from farther north (e.g., Fig. 9), and it is equally distinct from the northernmost specimens of *D. oreas* from an adjacent

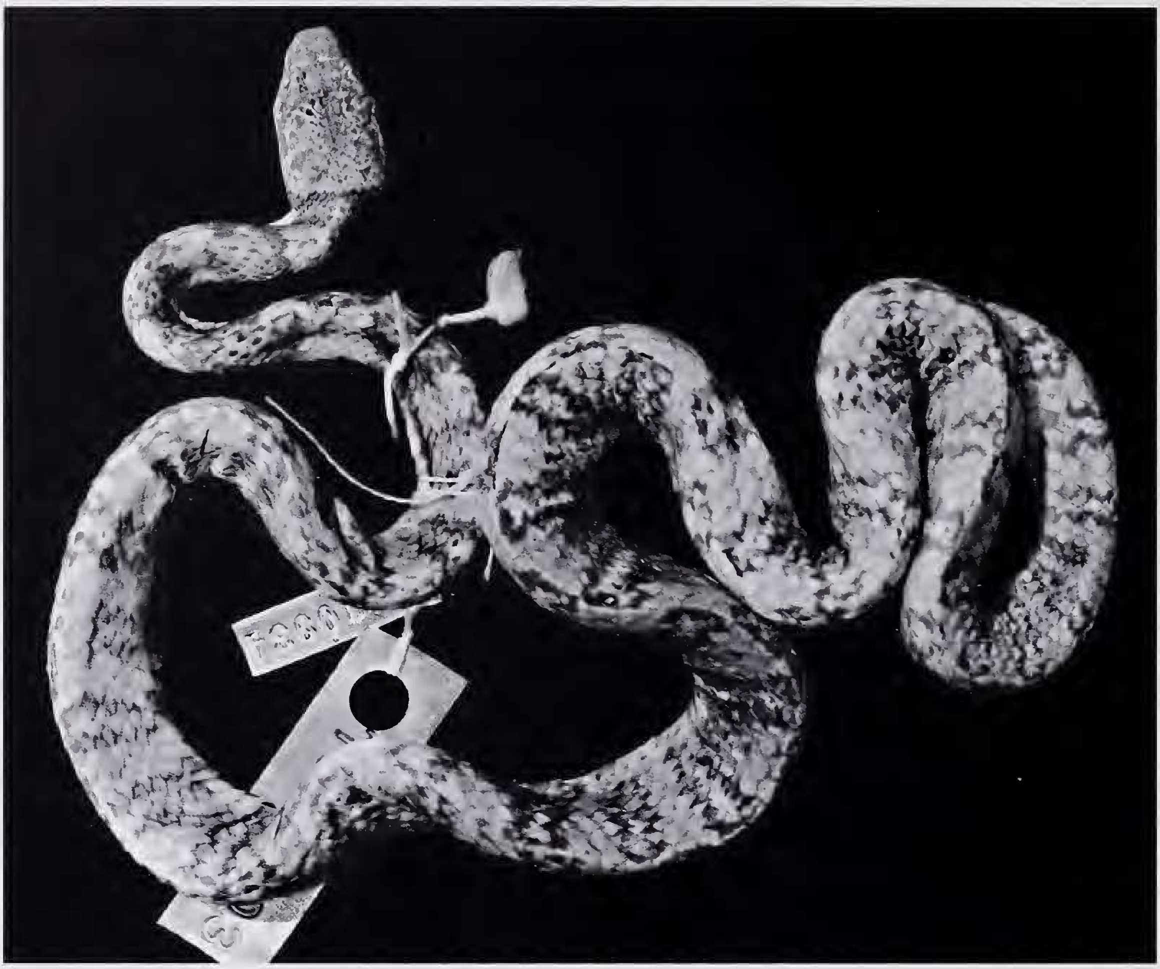

Figure 9. *Dipsas elegans* (Boulenger). Dorsal view of an adult male from Pichincha Province, Ecuador (USNM 210934, 501 mm SVL).

valley (see Fig. 8, localities 14, 16–17). The scutellation and body proportions of *D. elegans* and *D. oreas* are similar, whether the reference sample of *D. oreas* includes only Ecuadorian specimens (the most pertinent comparison to *D. elegans*) or the entire sample of *D. oreas* from Ecuador and Peru (Table 1). Average subcaudal number in male *D. oreas* is significantly less than in male *D. elegans* and their ranges do not overlap. Other segmental counts are similar between the two species, although average values differ (Table 1).

An additional characteristic distinguishing *Dipsas elegans* and *D. oreas* is an unusual pattern of sexual dimorphism in *D. elegans*. *Dipsas elegans* is strongly sexually dimorphic in both ventral and subcaudal counts, whereas *D. oreas* is sexually dimorphic only in subcaudal counts (Table 1). Additionally, the pattern of sexual dimorphism in ventral counts in *D. elegans* is observed infrequently among colubrids: male *D. elegans* have significantly greater numbers of ventral scutes than females (Table 1), the reverse of the common pattern in snakes (Shine, 1993).[5] In contrast, the pattern of sexual dimorphism in subcaudal counts in *D. elegans* is typical of the general pattern in colubrids; males have significantly greater subcaudal counts than females, and the ranges of subcaudal counts for males and females are entirely nonoverlapping.

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[5] Species in which male ventral counts are greater than in females are uncommon, but this is a derived character for some putative clades, such as the Neotropical xenodontine tribe Tachymenini (*Tachymenis, Thamnodynastes, Tomodon, Pseudotomodon, Ptychophis, Gomesophis,* and *Calamodontophis*; Bailey, 1967, 1981). The relationships of the Tachymenini are unclear, but no specific relationship to the Dipsadini or Dipsadinae is indicated, despite similarities among some of the included species, such as male superiority in ventral number and a propensity to consume gastropods in Dipsadini and some Tachymenini, for example, *Tomodon* (Bailey, 1981; Gallardo, 1972, and references therein). Some other genera

A few other subtle characteristics also distinguish *Dipsas elegans* from *D. oreas* (characteristics given first for *D. elegans* followed by those for *D. oreas*; Table 1): Maxillary tooth number (17–21 vs. 12–14), number of bands/blotches on the body (26–46 vs. 17–30), supralabials touching the eye (usually 2 vs. usually 3, but these patterns are highly variable), and loreal pattern (pattern 3 predominant, or pattern 4 vs. patterns 1 and 2 predominant, or patterns 5 or 6). Despite these other differences, color pattern is the most obvious accessible difference between *D. elegans* and *D. oreas,* and it is distinctive except for small juveniles (approximately <200 mm SVL) of both species, which are similarly patterned with solid bands (Figs. 11, 12, 17). In such cases, careful attention to sex, scutellational variation, head color pattern (see below), and maxillary tooth number is usually decisive in differentiating these species. See additional comments on comparisons of juvenile color patterns of these two species below (*Color and Pattern of Juveniles in Preservative*).

## Description

Variation in standard systematic characters for *Dipsas elegans* is summarized in Table 1.

*Size, Scutellation and Dentition.* The largest specimen is a female 782 mm total length, 587 mm SVL. Largest male 683+ mm total length (tail incomplete), 515 mm SVL. Tail 26–28% of total length in males, 22–26% of total length in females. Body strongly compressed. Dorsal scales usually in 15-15-15 rows, but 3 of 14 specimens examined showed a posterior reduction to 13 rows, and one specimen each had the unusual patterns of 15-17-16 or 16-15-15 rows (see Peters, 1960a: 90, for additional discussion). Vertebral scale row 1.5–2× the width of paravertebral rows, relatively wider in juveniles than adults. Ventrals 177–189 (averaging 181) in eight males, 166–178 (averaging 172) in five females. This pattern of sexual dimorphism is the reverse of the common pattern in colubrids (see footnote 5). One or two preventrals precede the ventral series (see Myers, 2003, for discussion). Subcaudals 94–105 (averaging 98) in six males, 68–88 (averaging 80) in five females. Total segmental counts 272–294 in six males, 237–260 in five females. Usually an elongate loreal and a small preocular bordering the anterior edge of the eye (Fig. 1: loreal pattern 3); preocular superior to loreal. Preocular sometimes fused with the prefrontal, resulting in loreal pattern 4 (Fig. 1). Head scales variable: postoculars usually 2 (occasionally 1); primary temporals usually 2 (range 1–3); secondary temporals usually 3

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of Tachymenini consume lizards or frogs (Bailey, 1981; personal observations). Among other putative synapomorphies, genera of Tachymenini are viviparous (stated as oviparous by Bailey [1967] but corrected by Bailey [1981]).

On the basis solely of hemipenial morphology, Zaher (1999) left the position of the Tachymenini as "Dipsadinae incertae sedis," and other workers have concluded that they "appear to be dipsadines" (e.g., Harvey and Muñoz, 2004). However, this association is contradicted by biochemical data (Cadle, 1984a; Vidal et al., 2000), which clearly ally three of the genera (*Thamnodynastes, Pseudotomodon, Tomodon*) to the South American xenodontine clade of Cadle (1984a) (=Xenodontinae of Zaher [1999] in large part). Although these genera lack the two hemipenial synapomorphies of "Xenodontinae" *sensu* Zaher, they similarly lack synapomorphies of Dipsadinae except, in some species, a relatively distal division of the sulcus spermaticus. However, this character varies within some colubrid genera, including Tachymenini (e.g., *Thamnodynastes* and *Tachymenis* among the Tachymenini), *Taeniophallus* (Xenodontinae according to Cadle [1984a], Myers and Cadle [1994], and Vidal et al. [2000]; incertae sedis according to Zaher [1999]), and *Geodipsas* (Pseudoxyrhopinae *sensu* Zaher, 1999). Hemipenial morphology evolves just as other anatomical characters, and it is highly unlikely that all species of large, diverse clades such as Dipsadinae or Xenodontinae will retain all characters synapomorphic for the clades (=characters plesiomorphic within the clade).

(range 2–4); supralabials 6–9, usually with supralabials 4 and 5 bordering the eye, but this characteristic is highly variable (Table 1); infralabials 8–12. Either one pair ($N$ = 8) or two pairs ($N$ = 5) of infralabials in contact behind the mental. Two or three pairs of squarish chin shields, followed by one or two pairs of gular scales, which are often subequal and offset. Maxillary teeth 17–21 ($N$ = 12).

Most specimens of *Dipsas elegans* are from localities near the equator (Fig. 8), but specimens from the extreme ends of the distribution are, in some respects, unusual in some scutellation characteristics that may reflect geographic patterns (sample sizes are too small to analyze trends). BMNH 80.1.5.267 (Fig. 13), a female from the southernmost locality, Pallatanga (Fig. 8: locality 14), has the lowest subcaudal count (68) of all specimens (78–88 in other females), and a ventral count at the lower end of the range (169, compared with 166–178 in other females). I considered the possibility that this specimen might be *D. oreas*, in part because its locality is closest to the distribution of *D. oreas* (Fig. 8). However, its color pattern is typical of other *D. elegans* (details in the following section) and unlike the color pattern of *D. oreas.* Moreover, its ventral and subcaudal counts would be low for *D. oreas* as well. Other characteristics of this specimen are also more typical of *D. elegans* (see Table 1): maxillary teeth 17, two supralabials touching eye, and loreal pattern 4. A female (USNM 210939) from the next northern locality (Corazón, Fig. 8: locality 13) has the lowest ventral count of all females (166), but a subcaudal count (84) that is more typical for female *D. elegans.*

The northernmost locality for *Dipsas elegans,* represented by a male (UMMZ 92073), has both the highest ventral (189) and subcaudal (105) counts I recorded for this species. However, Orcés and Almendáriz (1987) reported the upper range of subcaudals for this species as 107 (sex and locality not given). These data for specimens at the northern and southern extent of the range of *D. elegans* suggest that higher ventral and subcaudal counts may pertain to the northern part of the range of the species, with lower counts in the southern part.

*Color in Life.* Unknown.

*Color and Pattern of Adults in Preservative.* In *Dipsas elegans,* the dorsal ground color is pale brown with a series of 26–46 dark brown bands and/or bars on the body, each marking having a pale center (Figs. 9, 13). The markings have more or less vertical edges and extend ventrally to the first scale row or the outer edge of the ventrals. Anterior markings are about 5 scales rows in width, narrowing to about 3 rows by midbody, and are usually complete across the vertebral region (there is frequent incursion of dark pigment middorsally so that the central pale areas are interrupted). Posterior bands are frequently offset middorsally, forming a series of lateral bars (Fig. 13). Interspaces anteriorly are narrower than the bands (approximately 3 scale rows) but are wider than the bands posteriorly (5–6 scale rows). The venter is dull grayish brown with a dense covering of dark brown squarish markings that tend to be concentrated toward the outer edges of the ventrals, sometimes forming longitudinal arrays. The dorsal pattern of *D. elegans* is essentially identical to that of *D. ellipsifera,* but the centers of the bands in *D. elegans* usually are a pale brown to tan (in preservative), rather than whitish, as in *D. ellipsifera.*

The top and sides of the head are marked heavily with irregular dark markings on a pale brown ground color (Fig. 10). The markings are so extensive in some specimens that most of the top of the head is a solid dark brown with occasional light areas of the ground color showing through. Juveniles tend to have more solidly dark-colored heads than adults. Upper and lower labials are pale brown with dark brown irregular spotting, often not concentrated along suture lines. Often the dark pigment on the supralabials is concentrated below

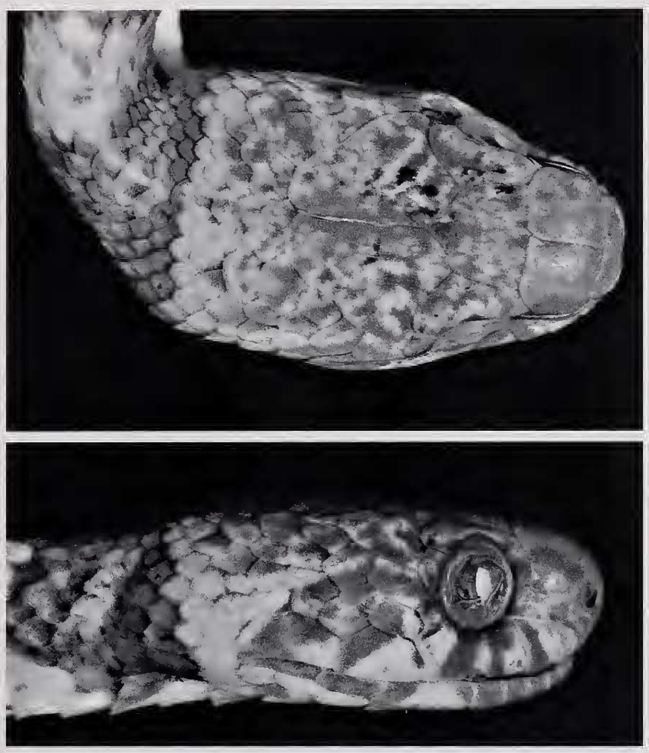

Figure 10. Head pattern in *Dipsas elegans* (Boulenger). Dorsal and lateral views of the head of USNM 210934.

the eye and on the posterior supralabials. In a few specimens, the dark pigment on the posterior supralabials extends diagonally toward the eye so as to form an irregular and indistinct postocular bar, but no individuals have a distinct postocular bar.

The following specimen is exemplary of the typical adult color pattern of *Dipsas elegans.*

*BMNH 80.12.5.267 (see Fig. 13; Pallatanga, Chimborazo Province, Ecuador. Female, 452 mm SVL).* Anterior bands 3.5 to 4 dorsal scale rows wide at their widest points; 2 rows wide at midbody and posteriorly. The first three dorsal bands and the sixth are complete middorsally; all others are incomplete and offset. The vertebral scale row is about 1.3× as wide as paravertebral rows. Dorsal blotches are dark-edged with pale centers, and more or less vertical (but jagged) edges. Interspaces are pale grayish brown, each scale heavily flecked with fine dark brown specks.

The top of the head is pale yellowish brown, marked with bold irregular spots all over; lacking the finer speckling that is present in most other specimens of *D. elegans.* The posterior edge of the head cap is marked with a narrow (1.5 scales wide) irregular edge in which dark pigment is more concentrated; following this is a pale nape collar about two scales wide, then the first neck band. Supra- and infralabials are pale with bold blackish marks, somewhat concentrated along suture lines.

The venter is heavily checkered with bold squarish blotches, with a slight tendency for these to align into irregular longitudinal streaks (but not as great a tendency as in some other specimens of *D. elegans*).

*Color and Pattern of Juveniles in Preservative.* The dorsal markings of *Dipsas elegans* apparently develop pale centers during early juvenile ontogeny, a phenomenon that also occurs in *D. oreas* (see subsequent species account). The dorsal bands of the juvenile holotype of *D. elegans* (223 mm SVL) already have light centers and a pattern similar to adults (see Kofron, 1982: fig. 1). Four smaller juveniles have bands in which there is no perceptible lightening: USNM 210938 (184 mm SVL), USNM 210961 (192 mm SVL), USNM 285957 (179 mm SVL), and BMNH 1940.2.20.32 (187 mm SVL) (Figs. 11, 12). Some lightening of the bands is apparent in two slightly larger individuals: in UMMZ 92073 (201 mm SVL; Fig. 12) lightening of the bands is barely apparent and is evident primarily on the anterior, wider bands; in USNM 210939 (199 mm SVL; Fig. 11), all of the bands have light centers. The last pattern is typical of adult *D. elegans* (Figs. 9, 13). Thus, small juveniles of *D. elegans* (<200 mm SVL) have solid bands, whereas the development of pale centers to the dorsal bands, and concomitant acquisition of adult color pattern, begins at approximately 200 mm SVL.

The following is a typical example of the color pattern of a small, solidly banded juvenile *Dipsas elegans* in preservative.

*BMNH 1940.2.20.32 (Río Saloya, Pichincha Province, Ecuador. Female, 187 mm SVL).* The dorsal pattern consists of regular, *solid* dark bands on pale ground color (no lightening of any dorsal bands). Bands are widest at midflank and narrow toward the ventrals and (less so) toward the vertebral scale row. Anterior bands are about 4 dorsal scale rows wide at their broadest point (the first band is 5 rows), narrowing to about 3 rows by midbody and continuing thus to the vent. Ventrally, the bands narrow to 3 scale rows wide on the anterior body, and to 2 rows wide on the posterior body; they encroach onto the outer edges of the ventrals.

The top of the head down to upper edges of supralabials is solid dark gray with a few scattered very indistinct irregular paler areas. Supralabials are about 50% covered with dark markings, which is not especially concentrated along sutures lines. Infralabials are mostly dark. An indistinct pale collar about 2 scales wide is between the dark head cap and the first neck blotch.

Ventral scutes are pale, with a pair of squarish blotches on the outer edges of most; the aligned blotches form irregular (and interrupted) series of broad lines on each side of the venter.

Small juveniles of *Dipsas elegans* with solid dorsal bands might be confused with juveniles of *D. oreas,* which also have solid bands. However, *D. elegans* typically has many more bands than *D. oreas* (compare Figs. 11, 12, 17), and the head patterns of the two species also provide differential characteristics. The top of the head in juvenile specimens of *D. elegans* is patterned with dark gray (?blackish in life) mottling

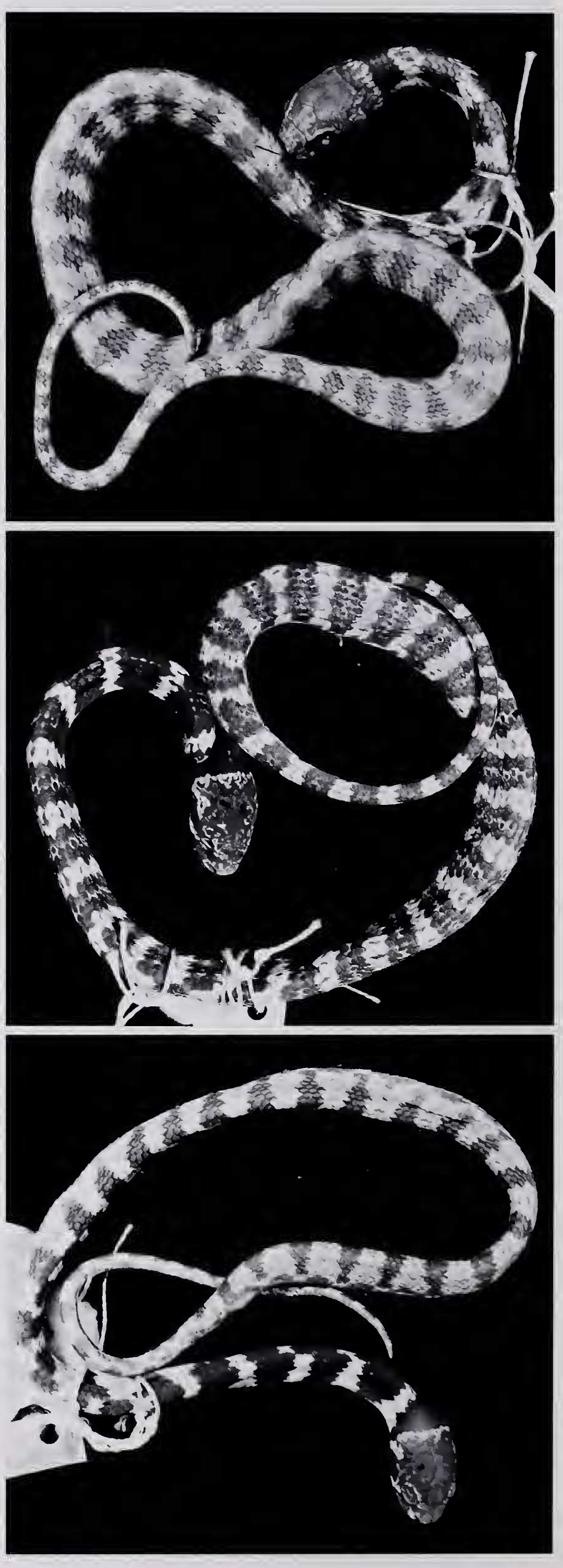

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Figure 11. Juvenile patterns in *Dipsas elegans* (Boulenger). **Top to bottom:** USNM 210961, 192 mm SVL (Pichincha Province, Ecuador); USNM 210939, 199 mm SVL (Cotopaxi Province, Ecuador); USNM 210938, 184 mm SVL (Cotopaxi Province, Ecuador). The two smaller specimens (top and bottom) show no perceptible lightening of the central parts of the bands, whereas the lightening is very apparent in the middle specimen.

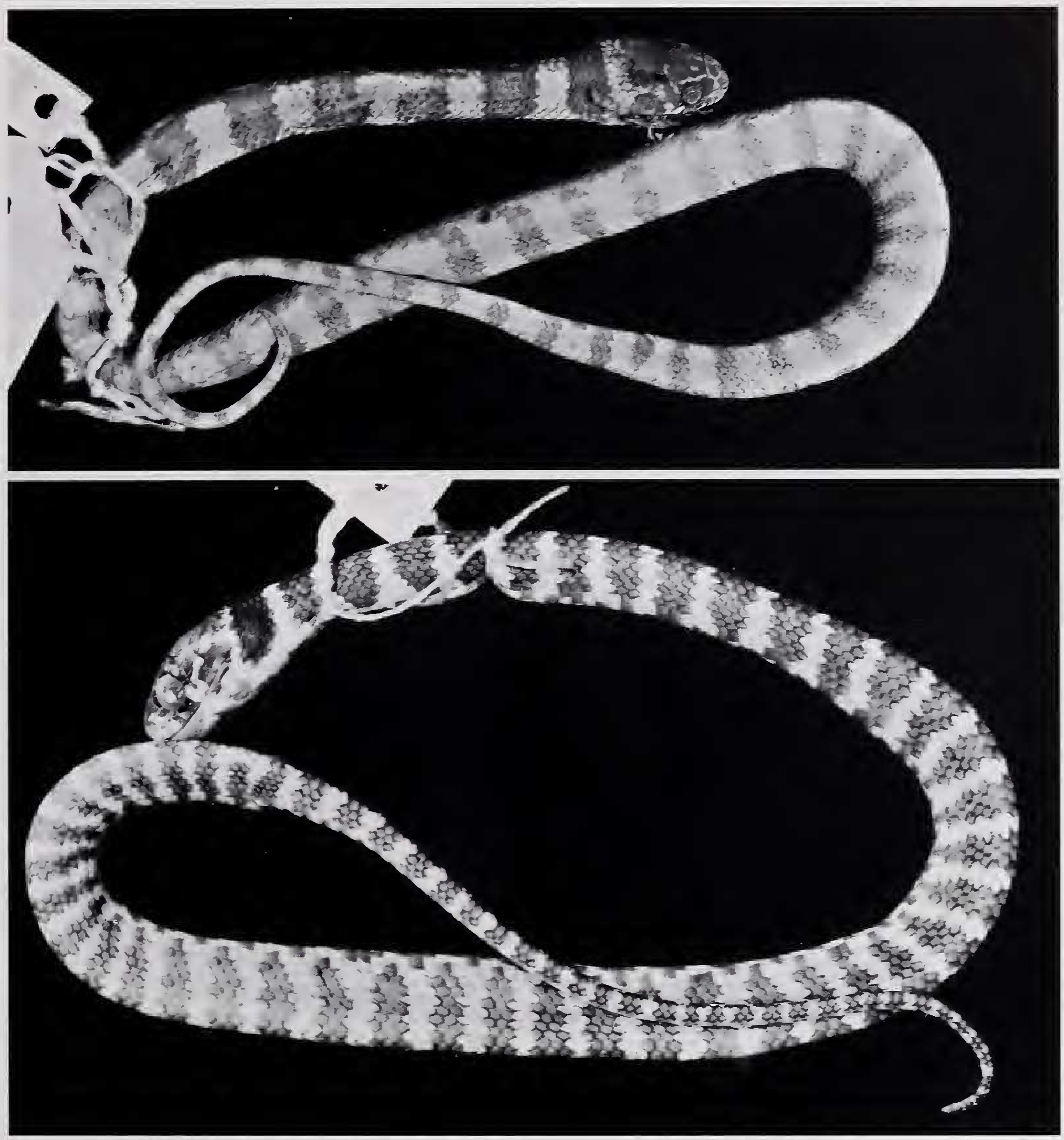

Figure 12. Juvenile patterns in *Dipsas elegans* (Boulenger). **Top:** UMMZ 92073, 201 mm SVL (Imbabura Province, Ecuador) showing some lightening apparent in bands on the anterior body. **Bottom:** USNM 285957, 179 mm SVL (Pichincha Province, Ecuador), in which no lightening of the central parts of the bands is apparent.

or reticulations on a pale brown or grayish ground color (the mottling may be so extensive as to color most of the top of the head with dark brown, especially in the parietal region). Juvenile *D. oreas* typically have paired dark elongate blotches in the parietal region, which is also characteristic of most adults (Figs. 16, 20; see also Cadle and Myers, 2003: 24, figs. 9, 10, 12). Moreover, juveniles of the two species differ by the other characteristics given in the diagnosis, including in loreal pattern (typically pattern 3 in *D. elegans*; typically pattern 1 or 2 in Ecuadorian *D. oreas*) and maxillary tooth number (Table 1). For example, maxillary tooth counts for seven juveniles of *D. elegans* (179–201 mm SVL) were 17–21; tooth counts for eight juveniles of *D. oreas* (150–193 mm SVL) were 12–14.

## Hemipenis

The hemipenes of the holotype of *Dipsas elegans* (BMNH 1946.1.21.77) had been previously exposed by ventral incision, and the right organ had been slit on its ventral surface. The following description is based on this specimen. It should be emphasized that, because the holotype is a juvenile, spines were not mineralized, and some other details perhaps differ from the adult condition (e.g., calyces appeared poorly developed, which might be either a product of the state of preservation or its juvenile condition, and spines in general had rather blunter tips than would be expected in a mature hemipenis).

The organ is very slightly bilobed at the tip (<1 mm), fully capitate, and extends to the level of the middle of subcaudal 8. The major retractor muscle is not divided at its insertion. The capitulum is ornamented with calyces bearing papillae; a distinct fringe of papillae borders the overhang separating the capitulum from the midsection. The capitulum appears to extend far less proximally on the asulcate than on the sulcate side and is more poorly delimited on the former. The sulcus spermaticus divides just inside the border of the capitulum. The midsection of the hemipenis has a battery of blunt spines (about 3–4 spines across, broader adjacent to the sulcus spermaticus than on the asulcate side). The blunt appearance of the spines is conceivably due to the juvenile state of the specimen; the more proximal spines in the battery have more pointed tips than more distal ones, possibly reflecting some mineralization of more proximal spines. Mineralization of the spines in colubrid hemipenes proceeds from proximal to distal on the organ (Cadle, 1996: 43–44; Myers and Cadle, 2003). Thus, it would not be surprising to observe more heavily mineralized spines on the proximal portion of a juvenile hemipenis.

The battery of spines is separated from the capitulum by a narrow gap of nude tissue (broader on the asulcate side). A poorly delineated but large basal nude pocket is present proximally; it is bordered distally by a pair of large spines, each of which is larger than any in the midsection battery, and a weakly developed lobe on one side. The proximal portion of the organ appears nude, but the presence of minute spines cannot be ruled out.

## Distribution and Natural History

*Dipsas elegans* is distributed in the lowlands and on the slopes of the Andes in western Ecuador from just north of the Equator in Imbabura Province (0°21′N) to approximately 2°S latitude (Fig. 8). Most localities are in the foothills or western slopes of the Cordillera Occidental, although Orcés and Almendáriz (1987) reported localities well over 2,000 m in upper reaches of the Río Guayllabamba east of the city of Quito (El Quinche, Cumbayá, and Tumbaco; Fig. 8: localities 10, 11). Recorded elevations for collecting localities are 500–1,820 m for specimens examined during this study, but localities reported by Orcés and Almendáriz (1987: 139) are higher: 1,500–2,643 m.

Two of four specimens that Boulenger (1896: 454) referred to "*Leptognathus mikanii*" variant C, which he considered equivalent to "*L. oreas*, Cope," are *Dipsas elegans*: specimens *c* and *d* from "W[estern] Ecuador" and "Pallatanga, Ecuador," respectively BMNH 60.6.16.73 and 80.12.5.267 (the other two, specimens *a* and *b* are, indeed, *D. oreas*). The Pallatanga specimen (Fig. 13) represents the southernmost record of *D. elegans* (Fig. 8: locality 14), and it has low ventral and subcaudal counts compared with other specimens (see *Description*).

A small juvenile (USNM 285957; 179 mm SVL) was collected 20 February 1979 "about 1900 hr near a small stream with waterfall along roadside; about 2 m up on the face of a road cut—moving on outer edge of vegetation about 15 cm from soil" (Roy W. McDiarmid, field notes). The specimens examined were collected in February, April, May, July, and October.

Orcés and Almendáriz (1987: 139) summarized the ecological circumstances for localities of *Dipsas elegans* as follows (see similar quotation in the account for *D. el-*

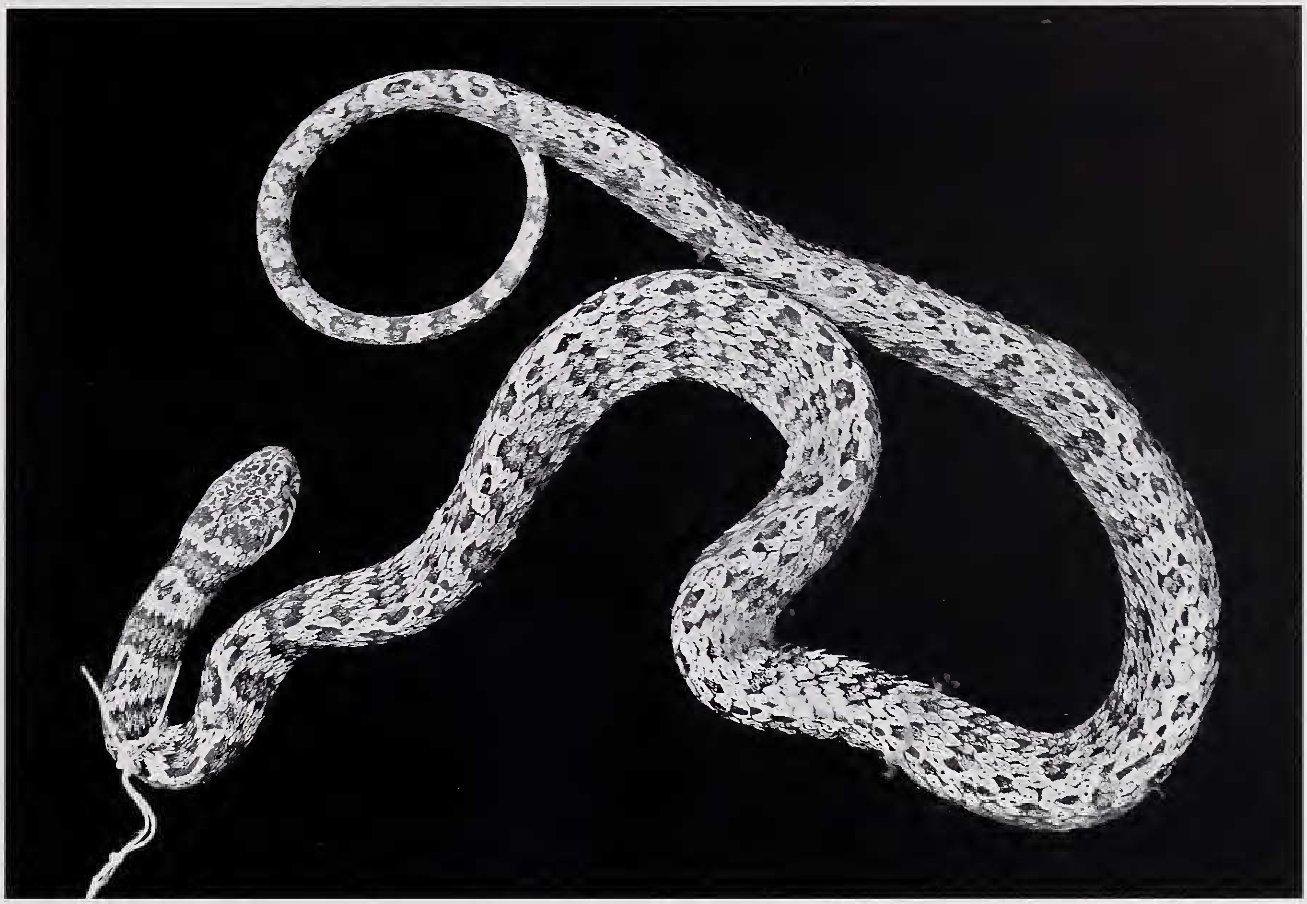

Figure 13. *Dipsas elegans* (Boulenger), an adult from Pallatanga, Chimborazo Province, Ecuador. This specimen represents the southernmost record for *D. elegans.* Boulenger (1896: 454) referred this specimen to "*Leptognathus mikanii,* variant C," which he considered equivalent to "*Leptognathus oreas* Cope."

*lipsifera*): "The ecological conditions are similar to those of the places inhabited by [*Dipsas ellipsifera*] but there are notable exceptions, for example Chiriboga [Pichincha Province] . . . has a very rainy climate and is covered with dense vegetation (according to the Holdridge Classification: Very Humid Lower Montane Forest), which in part has been destroyed through charcoal production." This characterization could well apply to higher elevation localities in the rain shadow valley of the upper Río Guayallabamba (Cumbayá, El Quinche, Tumbaco). However, many of the localities at lower elevations are in the area of western Ecuador that formerly was covered with primary lowland and lower montane rain forests before their major destruction during the last century (Chapman, 1926; Dodson and Gentry, 1991). It seems likely that these ecosystems were primary ones for *D. elegans.*

Orcés and Almendáriz (1987) reported a clutch of seven eggs of *Dipsas elegans* found in humid soil underneath decomposing logs in August 1987 at Chiriboga (Pichincha Province), Ecuador (Fig. 8: locality 12).

### ***Dipsas oreas*** **(Cope)**
### Figures 8, 14–23

*Leptognathus oreas* Cope, 1868: 109. Type locality: "the elevated Valley of Quito" (here inferred to be southern Ecuador; see discussion below). Holotype: ANSP 10115 (original number 6707 given in Cope's description, possibly the Orton expedition field number).

*Leptognathus mikani,* part: Günther, 1872: 29; 1885–1902: 141. Boulenger, 1896: 453, 454 (variant C, specimens *a, b* from "W. Ecuador"; =BMNH 60.6.16.56, 60.6.16.63; see Figs. 14, 22). Despax, 1911: 36.

*Leptognathus andrei*: Boulenger, 1896: 453. Kofron, 1982: 50.
*Sibynomorphus mikanii oreas*: Amaral, 1929a: 31; "1929"b [1930]: 198.
*Dipsas mikanii oreas*: Parker, 1934: 271; 1938: 444 [misidentifications] (at least in part =*Sibynomorphus petersi* and *S. oligozonatus*; Cadle, unpublished data).
*Dipsas oreas*: Peters, 1960a: 92. Miyata, 1982: 16.
*Leptognathus andiana*: Peters, 1960a: 92; 1965: 6. Resurrected from synonymy by Cadle and Myers (2003).
*Sibynomorphus andianus*: Peters, 1960a: 92.
*Dipsas oreas elegans*: Orcés and Almendáriz, 1987: 141. Pérez-Santos and Moreno, 1991: 154. Resurrected from synonymy herein.
*Dipsas oreas ellipsifera*: Orcés and Almendáriz, 1987: 141. Pérez-Santos and Moreno, 1991: 156. Resurrected from synonymy herein.

## Notes on the Holotype

The holotype (ANSP 10115; see photograph in Kofron, 1982: fig. 2) is an adult male in relatively good condition (somewhat soft and with the jaws dissected). Basic data are the following, with differences from Cope's (1868) description indicated in parentheses: Total length, 691 mm (26 inches [=660 mm]). Tail length, 182 mm. SVL = 509 mm. Tail as a proportion of total length, 26%. Dorsal scales in ?-15-15 rows (anterior body damaged). Vertebral row slightly wider than paravertebral rows. Ventrals, 178 (180). Subcaudals, 82 (90). Anal scale single. Preoculars, 0/0 (prefrontal and loreal bordering the anterior edge of the eye). Postoculars, 2/2. Temporals, 1 + 3/1 + 2. Loreal pattern 2/2 (prefrontal and loreal bordering eye). Supralabials, 7/7 with 3–5 touching the eye on each side. Infralabials, 11/11; one pair of infralabials in contact behind the mental scale. Three pairs of subequal squarish chin shields. The maxillary tooth count could not be done because the jaws are dissected and somewhat damaged.

Dorsal bands on body 23, those on the anterior half of the body complete middorsally; posterior bands are interrupted middorsally and moderately to greatly offset. Anterior bands tend to have squarish or angular edges, whereas posterior bands are more elliptical. All bands have some evidence of pale centers. Cope (1868) commented that the venter of the holotype was "largely obscured with black," but much of the venter is white (see Kofron, 1982: fig. 2). In an accompanying key, Cope used the alternative and more accurate phraseology "belly much black spotted" (Cope, 1868: 108). The black markings on the venter are squarish, and many are aligned to form longitudinal arrays.

## Diagnosis

*Dipsas oreas* is characterized by a moderate number of ventrals (167–184) and subcaudals (males, 82–91; females, 70–83) and a low number of maxillary teeth (12–14). It is a grayish to brownish snake with distinct bands and/or blotches that extend ventrally to the lateral edges of the ventral scales (Fig. 14). At least one, but usually more, complete bands are present on the anterior body, but posteriorly the bands tend to break up into a series of lateral blotches (often offset). The anterior bands are usually squarish, longer than tall, and broader than the interspaces; posterior bands are narrowed, sometimes reduced to vertical bars, and much narrower than the interspaces. In adults the centers of the bands are lighter than peripheral portions, but the lightening is never so extensive as to produce immaculate centers (i.e., scales in the central portions always retain dark flecks or spots). In a few specimens, most of the central portions of the bands is lightened so that the bands are distinguished by their darkened borders only (see Fig. 19). In this regard, Peters' (1960a: 33, 1960b: 515) "key" character that the bands in *D. oreas* are "never so light that the [bands] resemble paired ellipses" is occasionally violated. Nonetheless, the bands in *D. oreas* never attain the form of those in *D. elegans* or *D. ellipsifera*, in which the central parts of the bands are sometimes immaculate white. In small juvenile *D. oreas*, the bands are solid (without pale centers), and some adults are relatively unicolored posteriorly (Figs. 15, 19).

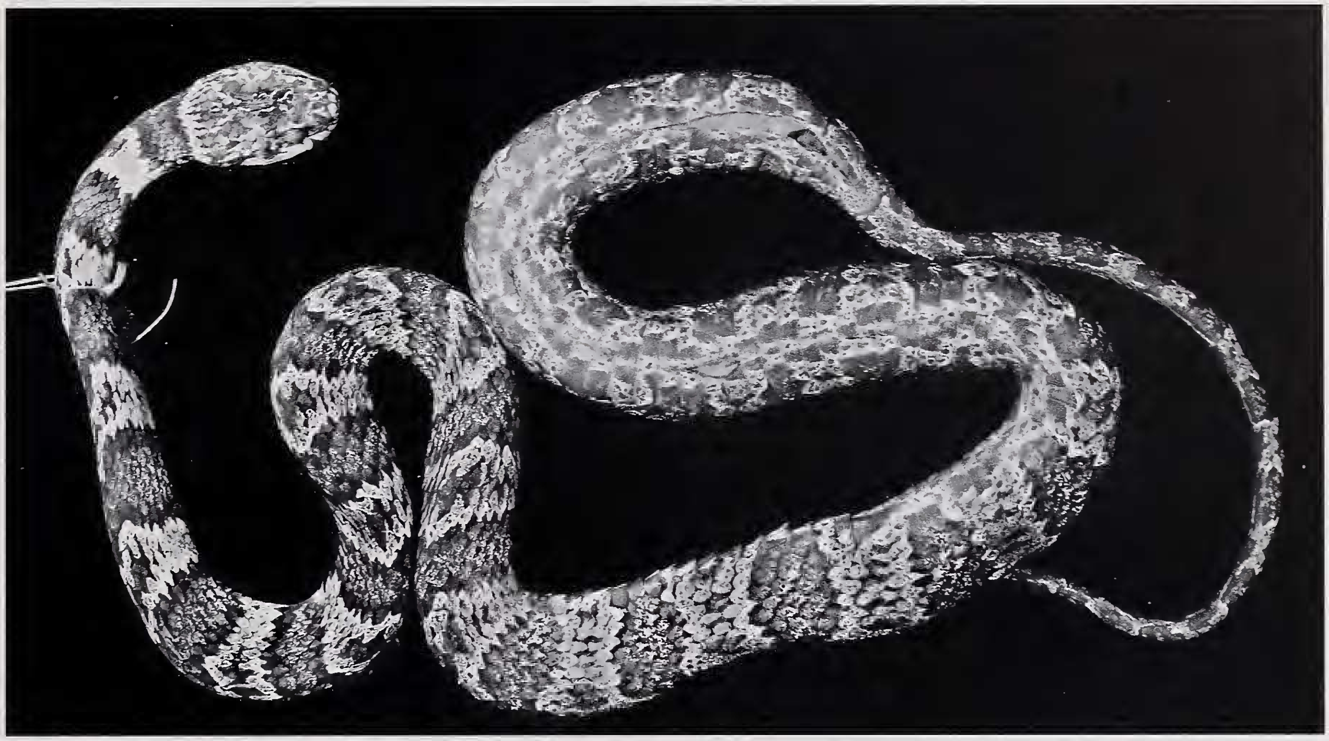

Figure 14. *Dipsas oreas* (Cope). Specimen from an unknown locality in western Ecuador showing a typical dorsal and posterior ventral pattern (BMNH 60.6.16.56; see Fig. 22 for detail of head). Ecuadorian specimens of *D. oreas* have narrower anterior bands than Peruvian specimens (compare Figs. 18, 19).

The top of the head in *Dipsas oreas* usually has an elongate blotch with irregular edges centered on each parietal scale and much additional irregular spotting or darkened suture lines on the head (see Fig. 20). The venter is usually strongly patterned with light and/or dark spots or squarish blotches, sometimes a checkerboard pattern or spots aligned in longitudinal arrays. See additional discussion and photos in Cadle and Myers (2003: 21–25).

*Dipsas oreas* is distinguished from other species of *Dipsas* in western Ecuador as follows. *Dipsas ellipsifera* has fewer ventrals (153–164) and subcaudals (62–78) and has a color pattern consisting of narrow vertical bands or bars with light (whitish) centers. *Dipsas elegans* has broadly overlapping scale counts with *D. oreas* (except male subcaudal counts; see Table 1) but has narrow vertical bands or bars with distinctly light (usually pale brown) centers (compared with the more subtle lightening in *D. oreas*), more maxillary teeth (17–21), and a different pattern of scales in the loreal region (see Table 1). *Dipsas oreas* has a high frequency of the preocular scale fused with the prefrontal, a rare condition in *D. elegans.*

*Dipsas andiana* has a distinctive U- or V-shaped marking on the top of the head and high numbers of ventrals (≥185) and subcaudals (≥91 in males, ≥80 in females; Cadle and Myers, 2003). *Dipsas gracilis* and *D. temporalis* differ from *D. oreas* in having very broad bands that are much wider than interspaces the entire length of the body, the anterior bands encroaching broadly onto the ventral scutes or complete across the venter, and high ventral counts (187–210 in *D. gracilis*; 187–208 in *D. temporalis*) and subcaudal counts (94–128 in *D. gracilis*; 119–132 in *D. temporalis*). (Data for *D. temporalis* include upper ranges reported in Peters, 1960a).

As discussed in the species account for *Dipsas elegans,* the greatest difficulty is in distinguishing small juveniles of *D. oreas* and *D. elegans* because both have solid blackish bands without pale centers (Figs.

11, 12, 17). *Dipsas oreas* tends to have fewer bands than *D. elegans*. This character, in combination with others, is decisive in species determinations. For example, ANSP 18123 has a somewhat atypical head pattern and high number of body bands (30) for *D. oreas*. However, other characteristics of ANSP 18123 are typical of *D. oreas* and quite unlike *D. elegans*: it has a low number of maxillary teeth (13) and loreal pattern 1 typical of *D. oreas* (pattern 3 or, rarely, pattern 4 in *D. elegans*; Fig. 1).

Apart from *Dipsas oreas*, the only other species of *Dipsas* definitely known from west of the continental divide in Peru is *D. gracilis*, which was recently reported from Tumbes department (Tello, 1998) and possibly occurs in Piura department as well. Another species, *D. latifasciata*, is known from immediately west of the continental divide in northern Cajamarca department. *Dipsas latifasciata* generally has more ventrals (179–194) and subcaudals (91–111) than *D. oreas* and more maxillary teeth (16–19), and the top of the head in *D. latifasciata* is generally solid black or with fine pale reticulations on a predominantly dark background. Notes on the distribution and taxonomy of *D. gracilis* and *D. latifasciata* are given later in this report.

## Description

The following description of *D. oreas* is based on variation summarized in Table 1, which gives additional details.

*Size, Scutellation and Dentition.* The largest specimen examined was a male 758 mm total length, 543 mm SVL. The largest female I examined was 732 mm total length, 566 mm SVL. However, Kofron (1982: 49) reported that the holotype of *Leptognathus andrei* Sauvage, a synonym of *Dipsas oreas*, was a female 827 mm total length, 626 mm SVL. Tail 25–28% of total length in males, 21–24% in females. Body strongly compressed. Dorsal scales typically in 15-15-15 rows, although other patterns occur (Table 1). Vertebral scale row slightly wider than, to 1.5× the width of paravertebral rows in adults, but relatively wider in juveniles. Ventrals 167–184 (averaging 176) in males, 167–181 (averaging 176) in females; hence, there is no sexual dimorphism in ventral counts. One to 3 preventrals anterior to ventral series (see Myers, 2003, for discussion). Subcaudals 82–91 (averaging 87) in males, 70–83 (averaging 76) in females. Total segmental counts 251–271 in males, 241–263 in females. Scales in the loreal region highly variable; often, both a loreal and a preocular border the anterior edge of the eye, but the preocular is frequently fused with the prefrontal and either the loreal or the preocular may be further divided. Loreal pattern typically 1 or 2, but high frequencies of patterns 5 and 6 occur, particularly in Peruvian specimens (Table 1, Fig. 1; see later discussion of geographic trends). Head scales variable: postoculars usually 2 or 3 (occasionally 1 or 4), primary temporals usually 1, 2, or 3 (rarely 4), secondary temporals usually 3 or 4 (range 2–4), supralabials 6–9, usually with supralabials 4–5, 3–5, or 4–6 bordering the eye, but these patterns are highly variable (Table 1). Infralabials 9–13 (usually 11 or 12 in Ecuadorian specimens, 12 or 13 in Peruvian specimens). Either one pair ($N = 23$) or two pairs ($N = 6$) of infralabials in contact behind the mental or one infralabial contacts two on the opposite side ($N = 9$); the frequency varies geographically, as discussed below. Two or three pairs of squarish, subequal chin shields; if only two pairs of chin shields are present, these are usually followed by one or two pairs of gular scales that are longer than wide. Maxillary teeth 12–14 ($N = 23$).

*Dipsas oreas* shows minimal sexual dimorphism in some characteristics that are commonly sexually dimorphic within colubrids. Males have only slightly longer tails than females when the total sample is considered, and there are no significant differences in ventral numbers between the sexes (Table 1). However, within the population sample from the Río Zaña Study Site, males have significantly longer tails than females (no difference in ventral number). Males average significantly greater subcaudal counts than females for both the "total" and "population" samples (Tables 1, 3). Females apparently attain greater body sizes than males in *D. oreas* (Table 1), but in the sample from the Río Zaña Study Site, the largest male and female were approximately the same SVL (Table 3). In the population from the Río Zaña Study Site, males and females apparently differ in the extent and manner of color change during growth (see next section).

*Coloration in Life.* Characteristic elements of color pattern in *Dipsas oreas* include (1) dark brown to black bands (wider than interspaces anteriorly, narrower posteriorly) on a grayish to pale brown ground color (bands usually broken into a series of lateral blotches on the posterior body), (2) a cephalic pattern usually involving a pair of large dark ovals centered on the parietal region and many other irregular dark markings, and (3) a venter that is usually dirty whitish with many dark squarish blotches (Figs. 14–19). The dorsal bands develop pale centers in larger snakes, the pale areas occasionally becoming so extensive as to obliterate most indications of bands (which remain as dark ellipses, the former edges of the bands). Some indication of bands was evident in all specimens examined, although bands are obscure in some large specimens (Fig. 19, bottom) because they nearly match the ground color. In these specimens, the bands are usually outlined with dark brown borders, and the anterior ones are usually more distinct than the posterior ones.

Except for brief notes (Cadle and Myers, 2003) no descriptions of coloration in life have been reported for *Dipsas oreas*. A specimen from southern Ecuador, KU 142803 (Cadle and Myers 2003: fig. 10), was described thus: "Dorsum tan with reddish brown blotches narrowly outlined with black. Venter cream with reddish brown spots. Iris tan" (field notes of Linda Trueb). In northern Peru, *D. oreas* shows considerable variation in coloration and pattern, and most variants can be found within a local area. Instances of extreme intrapopulational variation in color pattern are sometimes observed in other species of the tribe Dipsadini (e.g., Rossman and Kizirian, 1993). Nonetheless, the basic elements of the pattern are relatively constant in *D. oreas.* The variation is primarily due to greater or lesser emphasis on particular features of the pattern in different individuals. It is unclear whether such variation pertains to Ecuadorian populations because all Ecuadorian specimens examined have rather typical patterns in which the markings are rather bold. A moderately large sample of adults ($N = 10$) and juveniles ($N = 7$) from the Río Zaña Study Site makes it clear that ontogenetic change and, perhaps, sexual dimorphism account for some of the color variation in this species in northern Peru.

I herewith describe individual specimens from northern Peru to characterize some of the variation. I then describe the color pattern of a series of juveniles from the Río Zaña Study Site and discuss apparent patterns of ontogenetic change and sexual dimorphism. Color descriptions from life are taken from my field notes. Some of the pattern variants are illustrated in Figures 14–22; additional photographs of specimens of *Dipsas oreas* are found in Kofron (1982: fig. 2) and Cadle and Myers (2003: figs. 10, 11).

*ANSP 31777 (Figs. 15, 19, 20; Río Zaña Study Site. Adult Female, 548 mm SVL).* This is basically a brown snake with some obscure bands anteriorly, which fade posteriorly. The top of the head is medium brown with indistinct darker brown markings. Iris brown with lighter flecks. The upper labials are dull white, but heavily suffused, with medium brown concentrated along sutures and the upper parts of the scales. Lower labials are white with brown markings, but not so concentrated as on upper labials. Anterior 40% of body with broad brown bands that are most distinct anteriorly and fade posteriorly. Ground color between the bands is medium brown (as on the top of the head). Each band has darker brown anterior and posterior borders, with the band center about the same shade as the

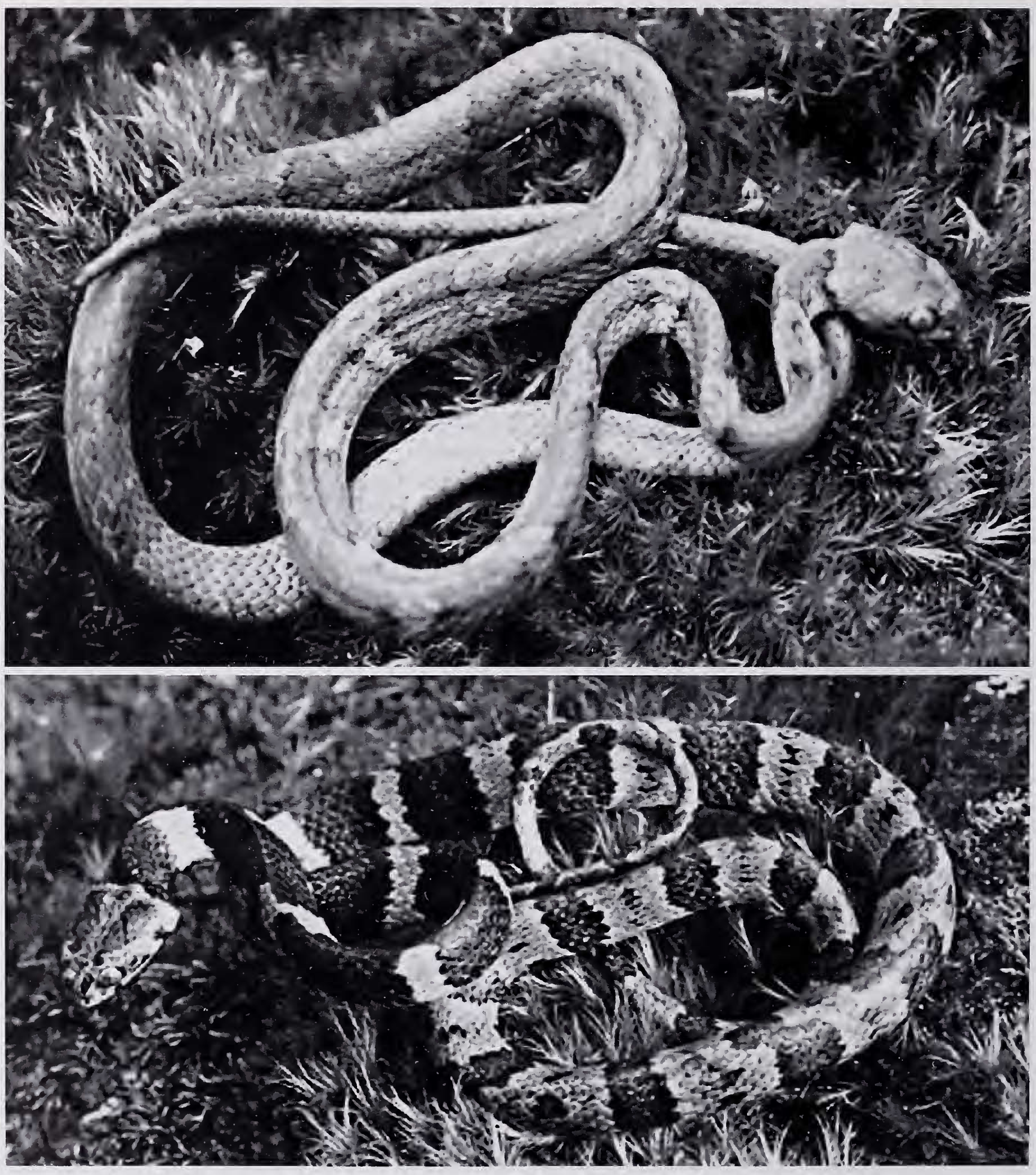

Figure 15. *Dipsas oreas* (Cope) in life from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** a female with a dorsal pattern showing little contrast (ANSP 31777). **Bottom:** a male with a highly contrasting dorsal pattern (ANSP 31778). Note also the difference in the distinctness of the cephalic blotches (see Fig. 20). The male is in a defensive posture (Cadle and Myers, 2003: 36).

interspaces. The bands continue onto the lateral third of ventral plates. Posteriorly the bands become narrower and fade gradually, although they can be distinguished to the vent (the darker edges disappear after the first 10 bands). The tail is uniform medium brown. The venter is dull whitish but flecked heavily by grayish brown, flecking increasing posteriorly.

*MUSM 5533 (Río Zaña Study Site. Adult Male, 472 mm SVL).* The color is essentially as in ANSP

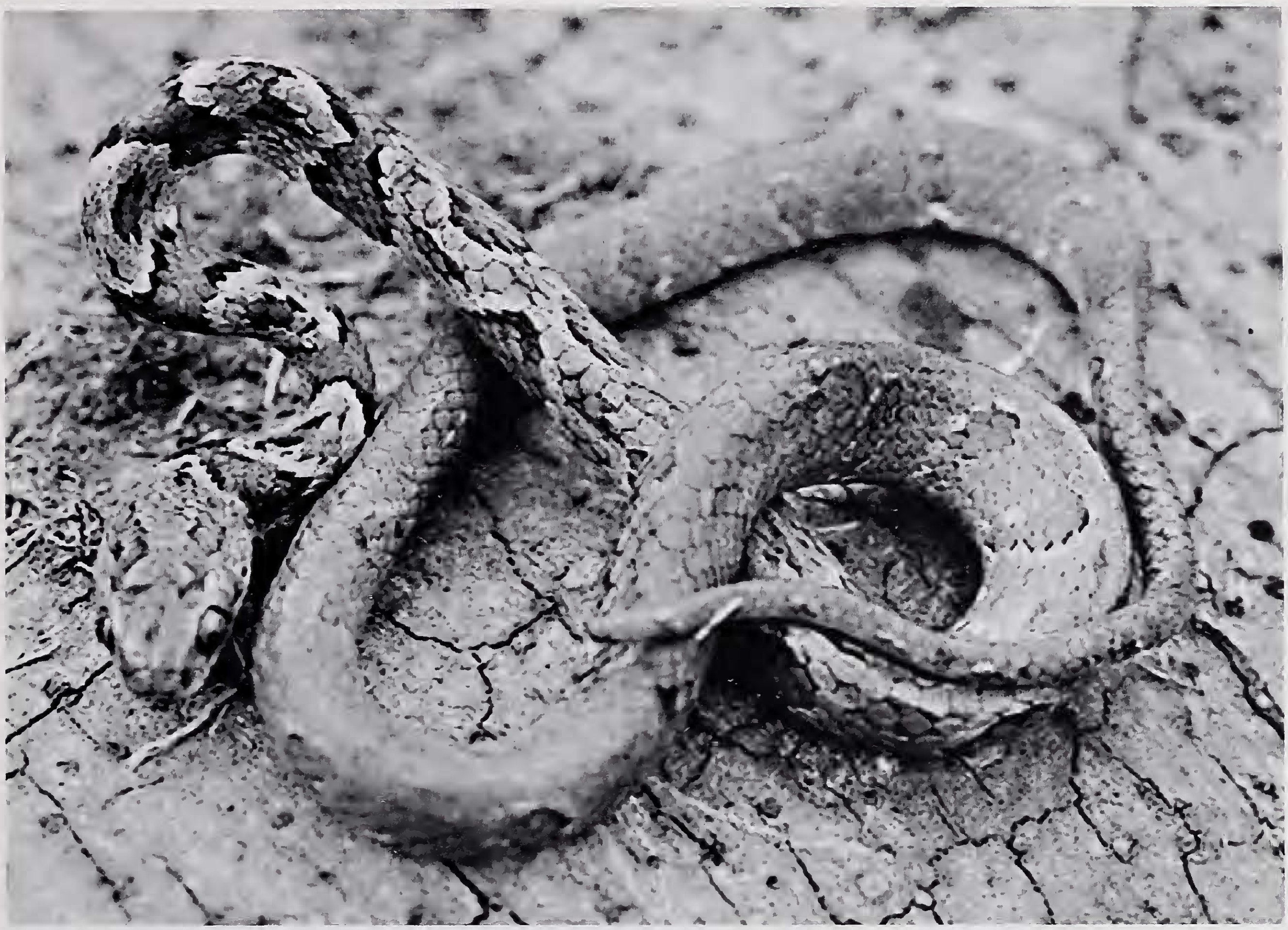

Figure 16. *Dipsas oreas* (Cope) in life from northern Piura department, Peru (MUSM 16750). An adult female with a highly contrasting anterior pattern, a much less distinct posterior pattern, and irregular cephalic blotches. The bands in this specimen are more irregular than most specimens from northern Peru.

31777 described above but the pattern is much more distinct. Interspaces between the dorsal bands are grayish brown, finely speckled with dark brown. Interspaces are much lighter than the center of the bands (compare ANSP 31777). Bands continue onto the tail, where about six can be distinguished. The bands tend to fade posteriorly, but they remain much more distinct than in ANSP 31777.

*ANSP 31778 (Figs. 15, 18, 20; Río Zaña Study Site. Adult Male, 424 mm SVL).* This individual is patterned much more boldly than other adults, and more similar to juveniles in the distinctness of the pattern. Interspaces light grayish brown. A series of black bands begins on the nape. The bands tend to have lighter (brown) centers, but this is not distinct except posteriorly. Bands extend onto outer third of ventral plates. Interspaces on the posterior half of the body are hatched with black, tending to form broken vertical bars. The top of the head is grayish brown with heavy black marking on most scales. Large black ovals cover the parietals and small posterior head scales. Iris grayish brown. Upper and lower labials grayish white, flecked with black. Belly whitish, stippled with dark brown, the stippling becoming heavier posteriorly. Underside of tail white but heavily stippled with dark brown.

*MUSM 16750 (Fig. 16; Piura Department, Peru. Adult Female; 326 mm SVL).* The dorsal ground color is medium brown with darker brown bands. The contrast between the ground color and band color is strongest anteriorly and weak posteriorly, where the bands are indistinct because their color nearly matches the ground colors. The anterior bands are much broader than posterior ones and are irregularly bordered by dark brown; posterior bands are narrow (2–3 scale rows) and not bordered by darker pigment except as isolated flecks. The five anterior bands are complete across the vertebral region; the remainder occur as a series of lateral blotches. Twenty-three bands on left side, 25 on right, between head and vent. The top of head is brown with dark brown irregular flecks. A pair of broad dark brown (partially bordered with black) arcs on parietals. Iris brown. Upper labials whitish, suffused with brown dorsally and with some dark pigment along sutures. Lower labials, throat, and anterior belly whitish. Brown pigment

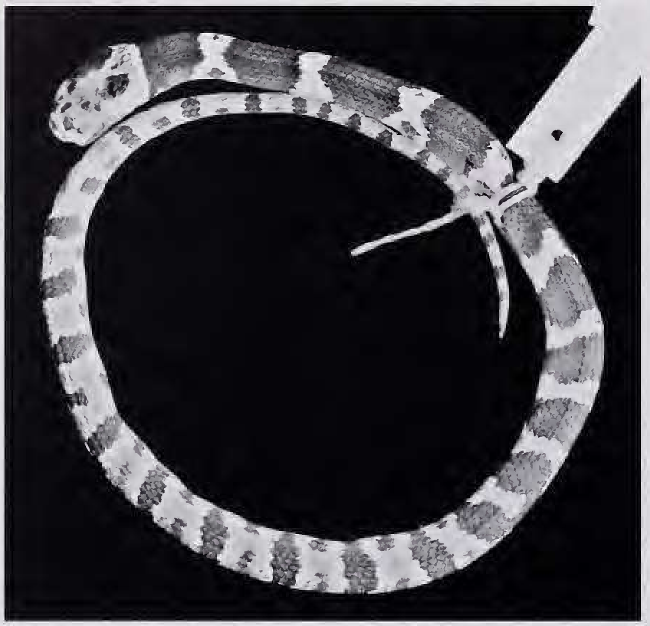

Figure 17. *Dipsas oreas* (Cope). A juvenile, solidly banded specimen from northern Peru (FMNH 232571, 163 mm SVL). Cadle and Myers (2003: fig. 11) illustrated two other juveniles.

increases posteriorly on belly, manifested by general darkening of ventral scutes. In addition, a series of brown (often white-bordered) bars is at the lateral edge of most belly plates. Small irregular ventrolateral markings are present on the outer edges of the ventral scutes, and lower dorsals often intercalated between dorsal (and lateral) bands. Tail coloration as in preceding body color.

*FMNH 232570–72, MUSM 16751–52 (Fig. 17; Río Zaña Study Site. Hatchlings).* Dorsum with broad black bands anteriorly, but narrower beginning at a point one-third to half way along the body. Bands tend to be offset posteriorly. Interspaces anteriorly are narrower than the bands, dirty white along the flanks, grayish brown with black pigment middorsally. Posterior interspaces are wider than the bands, grayish brown (somewhat lighter adjacent to bands), and with irregular black markings. In the posterior interspaces, and alternating with the bands, is a series of irregular squarish black blotches occupying the lateral edges of ventral scutes and part of scale row 1; there is one of these on each side per interspace. Top of head brown with irregular black pigment, mostly on parietals, prefrontals, and nasals. The elongate dark blotches characteristic of *oreas* are present in all specimens, but they tend to be somewhat more diffuse and fragmented than in many adults. The iris is grayish brown. Upper labials dirty white with a vertical black bar below the eye. Gular region dull white with some black spots on chin shields and anterior ventrals. Venter gray to brown, darker posteriorly, and irregularly peppered with tiny dark spots. Ventral surface of tail like posterior ventrals.

*Ontogenetic Change and Sexual Dimorphism in Color and Pattern in* Dipsas oreas. In contrast to the variation in color and pattern exhibited by adults of *Dipsas oreas,* hatchlings have a uniform pattern consisting of black bands and blotches on a white or gray ground color (Fig. 17; Cadle and Myers [2003: fig. 11] illustrate another hatchling from the same clutch of eggs). Most known hatchlings (i.e., specimens obtained from eggs hatched in the laboratory) are from the Río Zaña Study Site, the locality from which extensive color polymorphism in adults is documented. Other specimens within the size range of Río Zaña hatchlings or somewhat larger (e.g., ANSP 18120, 18123; MCZ 17083; UMMZ 56491; 150–193 mm SVL) all have solid bands. A still larger individual, USNM 98923 (292 mm SVL), has some evident lightening of the dorsal bands, as do all specimens with greater SVLs. Small juveniles and hatchlings of *D. oreas* of both sexes uniformly display similar color patterns, a contrast to adults.

Adult color patterns at the Río Zaña Study Site are highly variable. Some adults lose the highly contrasting pattern, whereas other individuals of comparable sizes retain contrasting patterns (Figs. 15, 18, 19). Adults that retain highly contrasting banding patterns are similar to juveniles except that the centers of the bands become lighter and the interspaces become more distinctly speckled with brown and/or black. Loss of highly contrasting dorsal coloration in some adults is apparently achieved by the interspaces and centers of the bands becoming invested with brown pigment, with only the borders of the bands retaining a much darker shade (blackish brown) than other parts of the dorsum (medium to light brown).

The differential expression of the pattern may be sexually dimorphic. The only two adult females from the Río Zaña Study Site (ANSP 31777, 31784; 548 and 551 mm SVL, respectively) are the largest individuals, and both lack highly contrasting dorsal colorations (Figs. 15, 19). Two adult

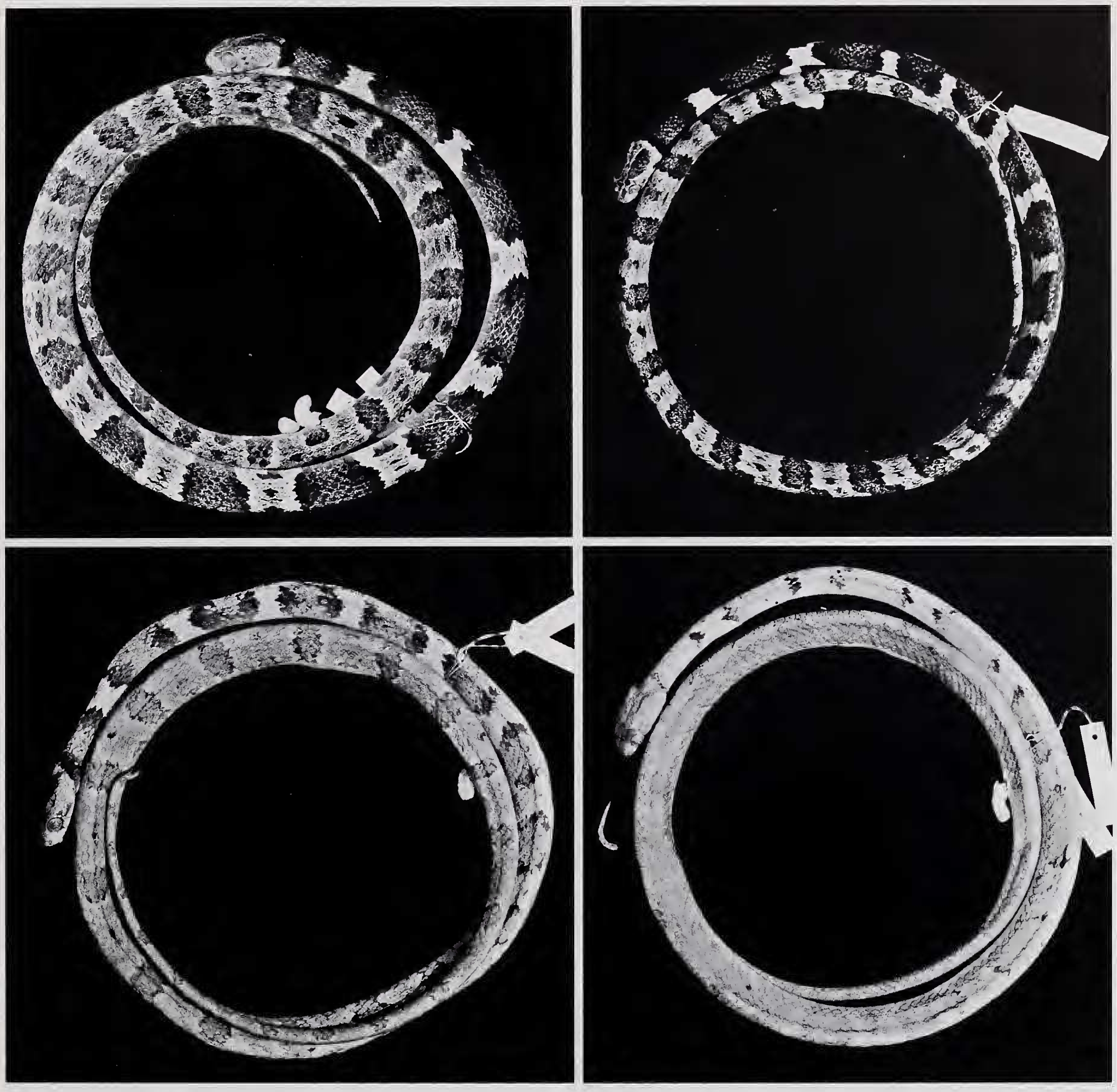

Figure 18. Variation in color pattern of adult male *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** left, ANSP 31779 (547 mm SVL); right, ANSP 31778 (424 mm SVL). **Bottom:** left, ANSP 31786 (543 mm SVL); right, ANSP 31780 (513 mm SVL).

males are of comparable sizes, but one (ANSP 31779; 547 mm SVL) retains a highly contrasting pattern, whereas the other (ANSP 31786; 543 mm SVL) is less contrasting but not as uniform as the two females (Fig. 18). Two smaller males (ANSP 31778, 31785; 424 and 506 mm SVL, respectively) retain highly contrasting patterns, whereas two others (ANSP 31780, 31783; 513 and 497 mm SVL, respectively) have reduced contrast (Fig. 18). A female (326 mm SVL) from another locality in northern Peru (MUSM 16750) has a highly contrasting pattern on the anterior body and much reduced contrast posteriorly (Fig. 16 and detailed color description above).

Thus, in the Río Zaña population, females possibly lose the highly contrasting juvenile patterns, whereas in males, the ex-

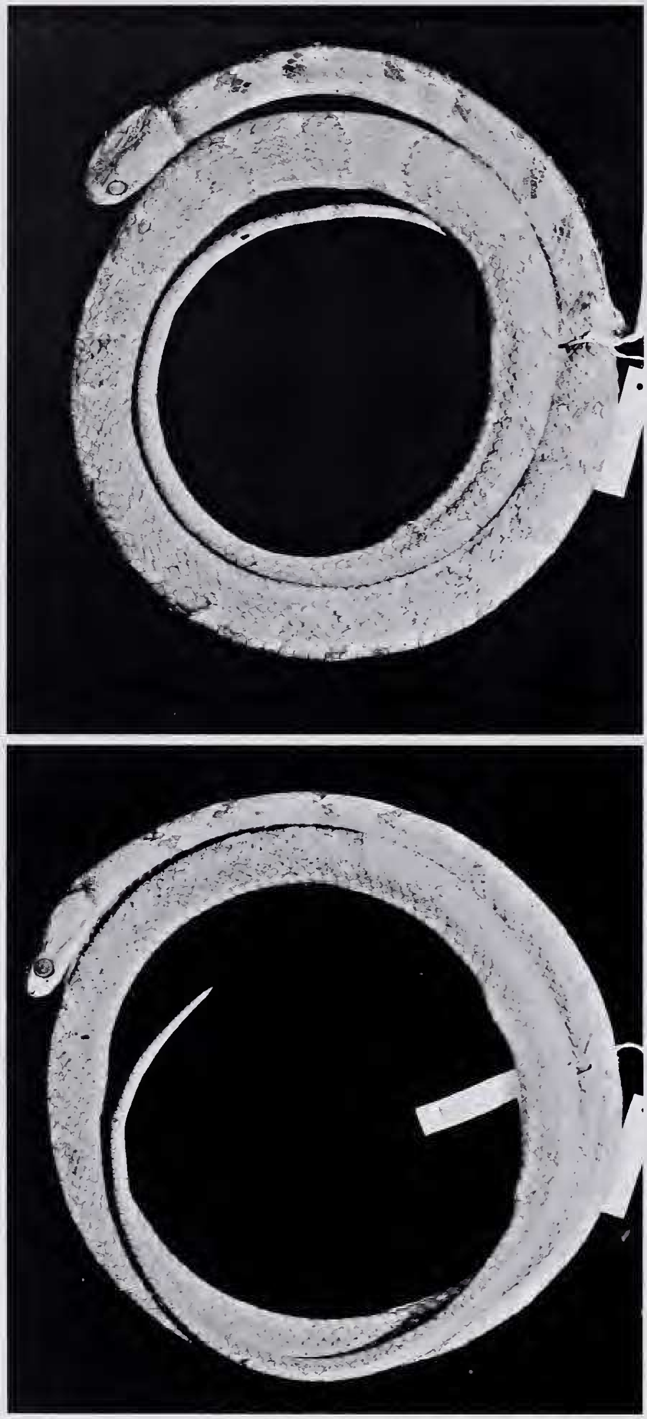

Figure 19. Variation in color pattern of adult female *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** ANSP 31777 (548 mm SVL). **Bottom:** ANSP 31784 (551 mm SVL).

pression of the contrast according to size is more variable. However, without larger samples and ontogenetic data on pattern changes, it is not possible to make definitive statements regarding sex or size differences in color pattern. It is also unclear whether the intrapopulational variation in color pattern at the Río Zaña Study Site applies to other populations. Sample sizes for different ontogenetic stages and sexes from single localities are insufficient to disentangle these effects from geographic or random variation patterns. Nonetheless, no examples of specimens with extremely pale bands or relatively unicolor dorsums are available from localities other than the Río Zaña Study Site.

*Color and Pattern in Preservative.* Preserved specimens retain the major pattern elements of live specimens, but colors become duller. Even specimens well over a century old (e.g., the holotype and BMNH 60.6.16.56; Fig. 14) have dark brown bands on a gray or grayish brown ground color. The lightening of the middle of the dark bands may become less evident in preservation, but most larger specimens retain even this sometimes subtle pattern characteristic.

Most specimens of *Dipsas oreas* have a pair of elongate oval blotches on top of the head from the level of the eyes to the nape (Fig. 20). These are more or less discrete, depending on how much additional black pigment occurs atop the head. Within the Río Zaña population, there is variation in the prominence of the blotches, just as in overall dorsal pattern (Fig. 20). Nonetheless, the characteristic form and presence of these cephalic blotches is a useful identifying characteristic for *D. oreas.* The lateral surface of the head is usually heavily and irregularly flecked with dark pigment, often concentrated along scale sutures and sometimes forming a more or less discrete diagonal postocular bar (Fig. 21).

Two specimens from unknown localities in western Ecuador, BMNH 60.6.16.56 and 60.6.16.63, have atypical head markings (Fig. 22). These lack distinct blotches on the parietals, although a pair of irregular blotches is evident on BMNH 60.6.16.56 that is similar to those on MUSM 16750 (Fig. 16). Instead, the top of the head is whitish but heavily marked with dark brown, resulting in a generally

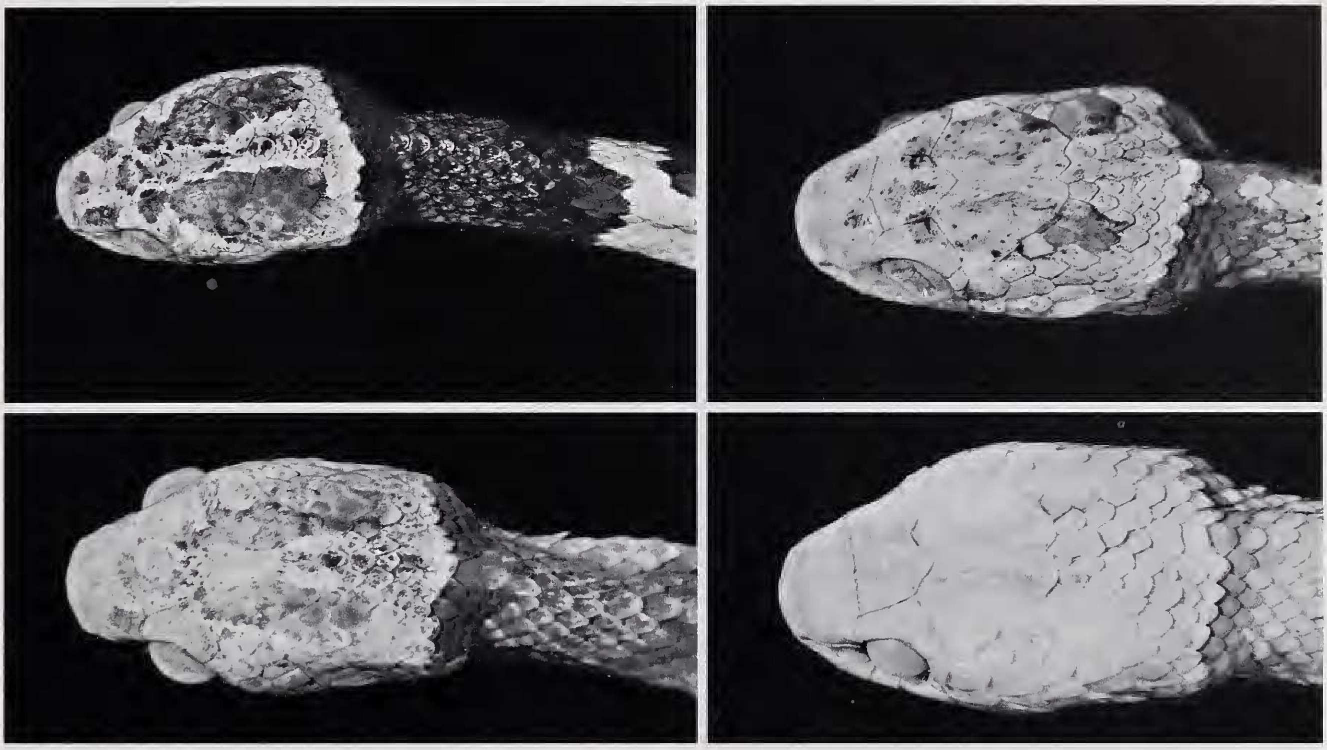

Figure 20. Variation in dorsal head patterns of *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** left, ANSP 31778 (male); right, ANSP 31786 (male). **Bottom:** left, ANSP 31779 (male); right, ANSP 31777 (female). The dark oval blotches centered on the parietal region are characteristic of most specimens of *D. oreas,* but vary within this population from very distinct to indistinct. In specimens that have very indistinct blotches (bottom right), at least the medial edges of the blotches are discernible by a dusky undulating border.

dark brown impression except under close inspection. The parietal scales of these specimens are irregularly marked with dark brown, which blends into the dark markings anteriorly and posteriorly on head. A few suture lines of the supra- and infralabials are marked with dark brown, especially anteriorly and posteriorly, but labial scales are rather unmarked compared with other specimens of *Dispas oreas.* Apart from the head patterns, the color patterns and other characters of BMNH 60.6.16.56 and 60.6.16.63 are typical of those seen in other specimens of *D. oreas* (Fig. 14).

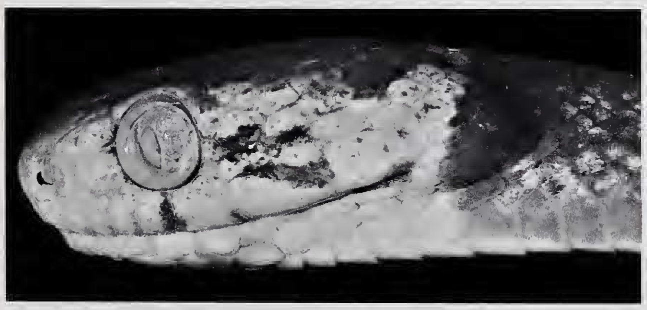

Figure 21. *Dipsas oreas* (Cope). Lateral view of the head of a specimen from the Río Zaña Study Site (Cajamarca department, Peru), ANSP 31785.

In a series of three specimens of *Dipsas oreas* from Chimborazo Province, Ecuador (ANSP 18117, 18120, 18123; adult female, juvenile female, and juvenile male, respectively), two show an obscure dorsal head cap without distinct parietal blotches, whereas the other (ANSP 18120; Cadle and Myers, 2003: fig. 11) has the parietal pattern typical of most *D. oreas.* In small juveniles, the parietal markings also tend to be more diffuse than in adults (Fig. 17 and above description of the coloration of hatchlings).

The venter of *Dipsas oreas* is usually moderately to heavily marked with large squarish spots or blotches, usually displaced toward the outer edges of the ventrals and sometimes aligned so as to form longitudinal arrays (Fig. 14). A few speci-

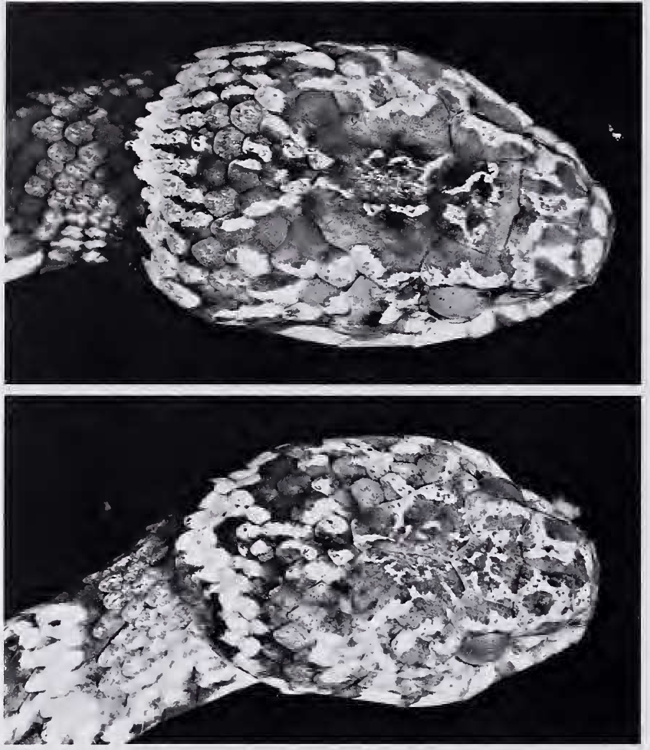

Figure 22. *Dipsas oreas* (Cope). Two specimens from unknown localities in western Ecuador with somewhat atypical head patterns. **Top:** BMNH 60.1.16.56 (see also Fig. 14). **Bottom:** BMNH 60.6.16.63. The cephalic blotches are less discrete in these specimens, in part because they are obscured by other irregular black and white mottling on the head.

mens (e.g., the holotype of *Leptognathus andrei* Sauvage illustrated by Kofron [1982: fig. 2]) have relatively unmarked venters.

## Hemipenis

The following description of the everted hemipenis of *Dipsas oreas* is based on specimens from northwestern Peru (ANSP 31778–81, 31783, 31785–86; all field everted). The organ is fully capitate, and the capitulum is calyculate and very slightly bilobed distally. The calyces are surmounted by a dense array of fleshy papillae. With the exception of the most distal papillae, the tips of the papillae are spinulate (i.e., they have mineralized tips). The sulcus spermaticus divides at the base of the capitulum and has centrolineal branches that extend nearly to the center of each of the small lobes. A large nude pocket approximately one third the length of the organ is on the lateral surface of the organ, extending from the base to the encircling battery of spines around the midsection. The pocket is bordered by a thick lobe on each side. These lobes are ornamented with tiny spines, but otherwise, the basal portion of the organ on both the sulcate and asulcate sides is nude or with scattered minute spines.

The asulcate side of the organ has a pair of extremely large spines just distal to the basal nude portion, distally followed by a gap ornamented with tiny spines and then a dense battery of large, thick spines occupying the midsection just below the capitulum. This battery encircles the midsection of the hemipenis, ending on the sulcate side short of the sulcus spermaticus, which has smaller spines adjacent to it. There is some variation in the width of the asulcate battery of spines. In most specimens, the battery is about 3 spines across, but in one (ANSP 31781), the battery has only 2 rows of spines in most places and only 1 row in the middle of the asulcate side; another (ANSP 31780) has 4 rows of spines throughout most of the battery (tapering toward the sulcate side). The spines in the midsection have very thick bases, taper abruptly distally, and end with a short hook at the tip.

The relative proportions of one of the organs (ANSP 31779) are: total length, 16 mm; bilobed distally for approximately 1 mm. The capitulum occupies approximately the distal 5 mm on the asulcate surface. Sulcus spermaticus divided distally for about 8 mm. Length of basal nude pocket, 5.5 mm. The hemipenes of these Peruvian specimens of *Dipsas oreas* are similar in detail to the everted organs of a specimen from Loja Province, Ecuador (KU 142803). In KU 142803 there is, in addition, a large spine just distal to the nude pocket.

## Geographic Variation in *Dipsas oreas* and *the Identity of Peruvian Specimens*

*Dipsas oreas* was previously documented in the Peruvian fauna in a brief note by Cadle and Chuna (1995: 32–33, footnotes

4, 5), who considered the species identification provisional at the time. Cadle and Myers (2003) discussed the species in resurrecting *D. andiana* from its synonymy; however, they did not specifically address the attribution of the Peruvian specimens to *D. oreas.* Some minor differences exist between the Peruvian and Ecuadorian specimens of *D. oreas,* but there is sufficient similarity to conclude that the range of *D. oreas* extends well into northern Peru. Nonetheless, some commentary concerning the referred Peruvian specimens is warranted. In assessing the following characterization of variation within Peruvian specimens of *D. oreas,* it is helpful to keep in mind that this sample is overwhelmingly dominated by specimens from the Río Zaña Study Site, which accounts for 17 of the 21 Peruvian specimens; thus, most of the variation within the "Peruvian sample" of this species actually represents intrapopulational variation within the Río Zaña Study Site population (Table 3).

There is a weak suggestion of a geographic cline in the number of dorsal bands on the body in *Dipsas oreas,* although samples are inadequate to analyze the trend thoroughly and are heavily weighted toward Peruvian specimens. Arrayed roughly north to south, the number of bands on the body in aggregated samples are (ranges followed by mean ± SD and sample size in parentheses):

Chimborazo Province +
"Western Ecuador":
22–30, 24.8 ± 2.73 (*N* = 7)
Guayas Province, Ecuador:
23–29, 25.3 ± 2.21 (*N* = 7)
Loja Province, Ecuador:
19–30, 24.5 ± 7.78 (*N* = 2)
Peru:
17–24, 19.7 ± 1.63 (*N* = 19)

Differences in the number of bands for these samples is mainly accounted for by the width of bands on the anterior body, which generally cover 8–10 dorsal scale rows in Peruvian specimens compared with only 5–7 rows in Ecuadorian specimens. Midbody and posterior bands are of similar widths throughout the range (usually 3–5 scale rows).

Ecuadorian and Peruvian specimens of *Dipsas oreas* also differ in some scutellation and other characteristics, but these are primarily average or frequency differences rather than discrete character differences. The differences between the "Ecuador" and "Total" samples of *D. oreas* in Table 1 are accounted for by the incorporation of Peruvian specimens into the "Total" sample summary (see also Table 3 for summary characteristics of a population sample from Peru). Ecuadorian specimens average higher numbers of ventral scales; have different frequencies of loreal, temporal, and labial scale patterns; and differ in modal number of maxillary teeth. All Ecuadorian specimens (*N* = 18) examined have a single pair of infralabials in contact behind the mental, whereas Peruvian specimens (*N* = 19) have either a single pair (*N* = 7), two pairs (*N* = 4), or one infralabial contacting two on the opposite side (*N* = 8).

Loreal pattern 6 (Fig. 1) was observed only in specimens from the Río Zaña Study Site (Peru), but in this population it occurred with high frequency (13 of 40 observations, considering each side of a specimen as an independent observation). A few specimens do not fit the discrete loreal patterns outlined. For example, UMMZ 56491 (Chimborazo/Cañar Province, Ecuador) has, on the left side, a small preocular that lies superior to an extension of the prefrontal intercalated between the preocular and the loreal scale; the prefrontal touches the eye at little more than a point. The right side of the same specimen has loreal pattern 2, but a partial suture on the posterolateral portion of the prefrontal is suggestive of a partially formed preocular scale. Variations such as this, and the similar relationship between patterns 3 and 4, give credence to the idea of a developmental relationship between patterns 1 and 2 on one hand and patterns 3 and 4 on the other. These apparent developmen-

Table 3. Scale counts, measurements (mm), and other data for the holotypes of *Dipsas oreas* (Cope) and *Leptognathus andrei* Sauvage (= *D. oreas*; data from Kofron, 1982: 49–50) and a population sample of *D. oreas* from Peru (Río Zaña Study Site). See Table 1 for separately tabulated data for *D. oreas* (Ecuadorian specimens and total sample). Bilateral counts for the holotypes are separated by a solidus (left/right). Data for the Río Zaña sample are summarized as in Table 1. *N* = Number of specimens or observations; SVL = snout to vent length.

| | *Dipsas oreas* holotype (ANSP 10115) Ecuador male | *Leptognathus andrei* holotype (MNHN 6285) Loja, Ecuador female | *Dipsas oreas* Peru (Cajamarca): Río Zaña study site |
|---|---|---|---|
| Total length (SVL) (mm) | | | |
| Largest male | 691 (509) | — | 758 (547) |
| Largest female | — | 827 (626) | 724 (551) |
| Tail length/total length | | | |
| Male | 0.26 | — | 0.26–0.28<br>0.27 ± 0.008 (*N* = 10) |
| Female | — | 0.24 | 0.21–0.24<br>0.23 ± 0.013 (*N* = 5) |
| Maxillary teeth | — | 14 | 13 (*N* = 1)<br>14 (*N* = 7) |
| Dorsal scales | ?-15-15 | 15-15-15 | 15-15-15 (*N* = 16)<br>15-17-15 (*N* = 1) |
| Ventrals | | | |
| Male | 178 | — | 167–180<br>173.2 ± 4.39 (*N* = 12) |
| Female | — | 178 | 167–178<br>172.0 ± 4.47 (*N* = 5) |
| Subcaudals | | | |
| Male | 82 | — | 83–91<br>87.4 ± 2.50 (*N* = 11) |
| Female | — | 79 | 70–81<br>75.6 ± 4.04 (*N* = 5) |
| Total segmental counts | | | |
| Male | 260 | — | 251–271 (*N* = 14) |
| Female | — | 257 | 241–259 (*N* = 5) |
| Anal scale | Single | Single | Single |
| Loreal pattern | 2/2 | 2/2 | 2 (*N* = 20)<br>5 (*N* = 1)<br>6 (*N* = 13) |
| Preoculars | 0/0 | 0/0 | 0 (*N* = 20)<br>1 (*N* = 14) |

TABLE 3. CONTINUED.

| | *Dipsas oreas* holotype (ANSP 10115) Ecuador male | *Leptognathus andrei* holotype (MNHN 6285) Loja, Ecuador female | *Dipsas oreas* Peru (Cajamarca): Río Zaña study site |
|---|---|---|---|
| Postoculars | 2/2 | 3/2 | 1 ($N$ = 3)<br>2 ($N$ = 13)<br>3 ($N$ = 18) |
| Primary temporals | 1/1 | 1/1 | 1 ($N$ = 2)<br>2 ($N$ = 18)<br>3 ($N$ = 13)<br>4 ($N$ = 1) |
| Secondary temporals | 3/2 | 3/3 | 2 ($N$ = 1)<br>3 ($N$ = 19)<br>4 ($N$ = 14) |
| Supralabials (touching eye) | 7(3–5)/7(3–5) | 7(3–5)/7 (3–5) | 6 (3–4) $N$ = 1<br>7 (3–4) $N$ = 1<br>7 (3–5) $N$ = 9<br>7 (4–5) $N$ = 8<br>8 (3–4) $N$ = 1<br>8 (3–5) $N$ = 2<br>8 (4–5) $N$ = 9<br>8 (4–6) $N$ = 3 |
| Infralabials | 11/11 | 9/10 | 10 ($N$ = 1)<br>11 ($N$ = 4)<br>12 ($N$ = 16)<br>13 ($N$ = 13) |
| Number of dorsal bands/ blotches on body[1] | 23 | About 31 | 17–22<br>19.7 ± 1.22 ($N$ = 15) |

Counts of body bands include only individuals having bands visible the entire body length.

tal relationships might explain a pattern of intraspecific variation in the *Dipsas oreas* group, whereby loreal patterns 1 and 2 or, alternatively, loreal patterns 3 and 4 tend to be characteristic of a species (Table 1).

All the scutellational differences and geographic trends are minor in view of the overwhelming similarities in both scutellation and color patterns between the Peruvian and Ecuadorian specimens of *Dipsas oreas.* However, the extensive variation in color pattern within and between populations of *D. oreas* in Peru (see discussion of color above) was not observed in specimens from Ecuador.

It is evident that the status of *Dipsas ellipsifera* and *D. elegans* relative to *D. oreas* has no bearing on the status of the populations of southern Ecuador and northern Peru here referred to *D. oreas.* All Peruvian specimens are referable to the nominotypical form of *D. oreas,* rather than to *D. ellipsifera* or *D. elegans,* as diagnosed herein. Orcés and Almendáriz (1987) noted that the range of "*D. oreas oreas*" extended farther south than the other subspecies but indicated that its distribution needed clarification. Their generalization appears to hold with the additional material examined for this study (Figs. 8, 23). *Dipsas ellipsifera* appears to be restricted to the Río Mira system of northern Ecuador, and I am unaware of specimens of *D. elegans* from south of central Ecuador (Fig. 8). In contrast, nominotypical *D. oreas* has previously been known south almost to the Peruvian border for more than a century (e.g., the holotype of *Leptognathus andrei* Sauvage from Loja). Hence, *D. elegans* and *D. ellipsifera* are not germane to evaluating the relationship of the Peruvian populations to nominotypical *D. oreas.*

## Distribution and Type Locality

*Dipsas oreas* is distributed from approximately 2°10′S (southern Chimborazo Province, Ecuador) to the Río Zaña in Cajamarca Department, Peru (6°51′S; Figs. 8, 23). Because of a copying error, Cadle and Myers (2003:43, fig. 10) referred KU 142803 to Pichincha Province, Ecuador. The coordinates given for the locality are correct, but the province is Loja.

Most specimens of *Dipsas oreas* come from the foothills and slopes of the western cordillera of the Andes (elevational range 1,400–2,900 m). However, a true lowland locality is represented by a series (USNM 60006, 62797–02) from "Guayaquil, Ecuador (sea level)," a locality that seems out of character not only in terms of elevation but also in terms of habitats at other known localities for this species (see Chapman, 1926, and subsequent discussion of habitats). Cadle and Myers (2003) considered the records from Guayaquil "probably in error." I am no longer convinced that the locality is erroneous, but only that it seems different from other known localities. The series was obtained from Dr. Frederick W. Goding, American Consul General in Guayaquil, and was catalogued about 1920. Goding obtained specimens of other species known from western Ecuador for the USNM during the same period. Several specimens of *D. oreas* from imprecise localities in the Río Chanchan valley due east of Guayaquil (ANSP, MCZ, and UMMZ specimens) could be from <1,000 m elevation, and it is not possible to unequivocably rule out lowland localities for this species on the basis of present knowledge.

At the Río Zaña Study Site, the documented elevational range of *Dipsas oreas* is 1,450–1,800 m. From the distribution of appropriate habitats in this local area (as of 1993), the elevational range may be much greater (1,400–2,500 m). It is very likely that the distribution of *D. oreas* becomes increasingly restricted to mesic and humid environments on the Andean slopes toward the southern end of its range because the lowlands along the northern Peruvian coast are primarily occupied by arid to xeric habitats (Chapman, 1926; Koepcke, 1961). Nonetheless, small parcels of humid lowland tropical forests in Tumbes department could harbor populations of

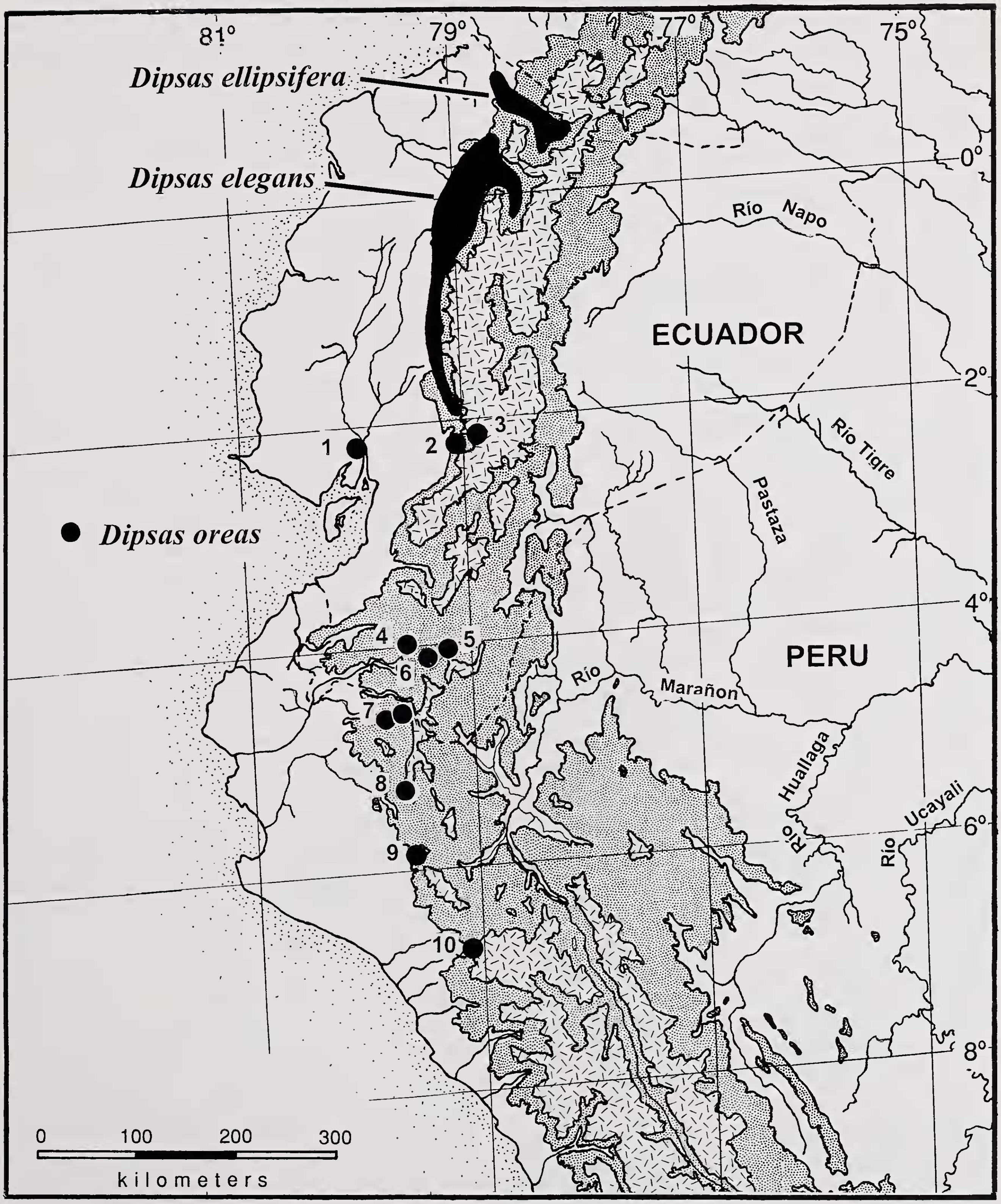

Figure 23. Ecuador and northwestern Peru showing summary distributions of *Dipsas ellipsifera* and *D. elegans* (based on locality records in Fig. 8), and locality records for *D. oreas* in Ecuador and northern Peru. Stippled area, above 1,000 m; hatched area, above 3,000 m. Numbered localities for *D. oreas* in Ecuador: **(1)** Guayaquil; **(2)** Huigra/Río Chiguancay and Río Chanchan valley; **(3)** Alausí; **(4)** Velacruz; **(5)** Loja; **(6)** Río Catamayo valley. In Peru: **(7)** Ayabaca and Cerro Aypate; **(8)** Canchaque; **(9)** Abra de Porculla; **(10)** Río Zaña Study Site.

*D. oreas* because another species, *D. gracilis,* has recently been discovered there (see later comments on *D. gracilis*).

Some known or suspected erroneous geographic records of *Dipsas oreas* in the literature bear some commentary. Parker's (1934: 271, 1938: 444) records of "*Dipsas mikanii oreas*" from the province of Loja in southern Ecuador seem to be based, at least in part, on misidentified specimens in the The Natural History Museum in London (BMNH) that I refer to *Sibynomorphus petersi* and *S. oligozonatus* (Cadle, unpublished data). Nonetheless, *D. oreas* is known from the province of Loja from other specimens (e.g., USNM 98923, KU 142803, and the holotype of *Leptognathus andrei* Sauvage). Fowler (1913: 169) referred three specimens to *D. ellipsifera* and *D. andiana* (ANSP 18117, 18120, 18123) that are here referred to *D. oreas* (Cadle and Myers, 2003: footnote 17, fig. 11). Peters' (1960a: 94, map 8) record of *D. oreas* from "Río Saloya" (Pichincha Province, Ecuador; Fig. 8: locality 7) is based on BMNH 1940.2.20.32, a juvenile here referred to *D. elegans.* Orcés and Almendáriz (1987: fig. 1) attributed the same locality to "*D. oreas oreas,*" probably based on Peters' record. Boulenger (1896: 454) referred four specimens to "*Leptognathus mikanii,* variant C (*L. oreas,* Cope)"; two of these (specimens *a* and *b,* BMNH 60.6.16.56, 60.6.16.63; Figs. 14, 22) from unknown localities in western Ecuador are *D. oreas,* but specimens *c* and *d* are *D. elegans* (see synonymy and distribution in the *D. elegans* species account).

On the other hand, Despax's (1911: 36) record of "*Leptognathus mikani*" from Alausí (upper reaches of the Río Chanchan valley, Chimborazo Province, Ecuador; Fig. 8: locality 17) probably correctly refers to *Dipsas oreas.* Despax (1911) stated that the specimen conformed to "Variant C" of Boulenger (1896: 454; ="*Leptognathus oreas*" Cope). In fact, Boulenger's "Variant C" included specimens of both *D. elegans* and *D. oreas* (see referred specimens in the synonymies given above for each species). However, *D. elegans* is not known from the region of Alausí, whereas *D. oreas* has been obtained by other collectors from the Río Chanchan valley (e.g., ANSP 18117, 18120, 18123; MCZ 17083; UMMZ 56491). Thus, it seems most likely that Despax's specimen is *D. oreas.*

With the above clarifications of literature records, it is clear that the northern limit of the distribution of *Dipsas oreas* is at approximately 2°S latitude. No confirmed records exist for *D. oreas* north of the Río Chanchan valley in southern Chimborazo Province. Additionally, there are no documented areas of range overlap for any of the three species of the *oreas* group (Fig. 8; contra Orcés and Almendáriz, 1987; Peters, 1960a). *Dipsas ellipsifera* seems likely to be restricted to the Río Mira basin and surrounding areas in northwestern Ecuador, whereas *D. elegans* is found to the south of that, along the western slopes of the Andes in northern and central Ecuador. Nonetheless, *D. elegans* is recorded from Pallatanga in the Río Chimbo valley (Chimborazo Province), the river system just north of the Río Chanchan valley from which *D. oreas* is known (Fig. 8: localities 14, 16, 17). The nearest localities for *D. elegans* and *D. oreas* (Pallatanga and Alausí, respectively) are separated by only about 26 km straightline distance (but also by a ridge >3,000 m). Thus, if there are areas of sympatry among any species of the *oreas* group, it seems most likely to occur between *D. elegans* and *D. oreas* in the region encompassing southern Bolívar/Chimborazo Provinces and adjacent areas of Guayas Province, Ecuador. Similarly, northern Imbabura Province (Fig. 8) is a potential area of contact between *D. elegans* and *D. ellipsifera.*

Most of the localities from which *Dipsas oreas* is documented are small remnants of once much more extensive humid forests (but see note below on a specimen from a dry semideciduous forest). In at least one instance, the locality near Porculla Pass

(Piura department, Peru) documented by MVZ 119330 (a road-killed specimen obtained in 1969), the population of *D. oreas* might be extinct. I visited the site in 1994 in an effort to sample remnant humid forests previously known to be extensive in this area (Koepcke, 1961). However, the easily accessible area had been completely denuded, except for a few trees remaining in steep ravines; a few small and highly fragmented forest remnants remain in this area (Sagástegui et al., "2003" [2004]). Most of the area is now very dry, and slopes are covered with grassland and occasional shrubs. I doubt that *D. oreas* and some other herpetofauna of humid montane forests of northwestern Peru (e.g., Cadle, 1989, 1991; Cadle and McDiarmid, 1990) can survive in such a habitat. The mid-1990s destruction of the forest of Monte Seco was mentioned above (see *Materials and Methods*). With continuing fragmentation and obliteration of these unique environments, endemics such as *D. oreas* will survive in increasingly smaller ranges or go extinct.

Curiously, despite the work of many herpetologists and other field biologists in western Ecuador, *Dipsas oreas* is known from relatively few specimens. Orcés and Almendáriz (1987) reported that the EPN collection contained no specimens, and Kofron (1982) stated that only eight specimens were known at that time. Recent brief biological surveys in southwestern Ecuador (e.g., Almendáriz and Carr, 1992) yielded no specimens of *D. oreas*. There is a distinct distributional gap between specimens collected in southern Chimborazo and Guayas Provinces (Río Chanchan valley and Guayaquil, respectively) and Loja Province to the south. However, few comprehensive collections are available from this area.

*Clarification of the Type Locality: Orton's "Valley of Quito."* James Orton was a naturalist and professor who obtained significant collections on several lengthy expeditions to South America, primarily Ecuador and Peru, in the 1860s and 1870s (Orton, 1875). Cadle (1989: 422–423) briefly summarized the Orton expeditions. The herpetological collections were turned over to Edward D. Cope of the Academy of Natural Sciences in Philadelphia, who catalogued the results of Orton's expeditions in a series of important papers on the herpetology of South America (Cope, 1868, 1874, 1876, 1877). Many species described by Cope (1868), such as *Dipsas oreas*, have the designated type locality "the elevated Valley of Quito," a vague statement that has been narrowly interpreted by most subsequent workers as the valley immediately surrounding the city of Quito, Ecuador (e.g., Peters, 1955: 347). Hence, "Valley of Quito" has often been questioned as a type locality for many reptiles described from Orton's collections because they are species unlikely to have ever occurred in that vicinity. However, Orton himself makes clear that his meaning was much broader, as noted by Orcés and Almendáriz (1987) and indicated in this quotation from Orton (1871: 620) and further amplified in his book (Orton, 1875: 152 ff.).

> The Valley of Quito . . . is a remarkably well-defined district, having a uniform temperate climate. It is nearly three hundred and fifty miles in length, stretching from 1°N. to 4°S., and has an average width of forty miles, being walled in by the grandest group of volcanic mountains in the world. These barriers have an average elevation of 12,000 feet above the sea, and are broken at few points, chiefly by the narrow gorges of the Santiago and Pastaza, and the sources of the Mira and Esmeraldos. The valley is subdivided by ridges into three basins—Quito, Ambato and Cuenca, having the respective altitudes of 9500, 8000 and 7500 feet. . . .

Thus, Orton's "Valley of Quito" comprised the entire Ecuadorian highlands from the Colombian border to the vicinity of Loja in southern Ecuador. The species described from this "locality," including *Dipsas oreas*, could have come from virtually anywhere in the Ecuadorian highlands or their western slopes. Cope (1868: 96) adds the following details, obtained directly from Orton, concerning the collections of 1867–68: "[The expedition] first touched the continent at Payta, Peru [=Paita], and afterwards at Guayaquil; then proceeded inland over the Andes to Quito; thence [eastward to the Río Napo]. . . . They collected Reptiles chiefly from Guayaquil, Pallatanga (on the west slope of the western Cordillera south of Chimborazo); Ambato (in Valley of Quito); western slope of the volcano Antisana, 13000 ft. above sea (a small black frog). . . .” A similar route between Guayaquil and Quito was followed by later naturalists (e.g., Samuel N. Rhoads) and resulted in specimens of *D. oreas* (e.g., ANSP 18117, 18120, and 18123 obtained by Rhoads; MCZ 17083, UMMZ 56491). Fowler (1913: 153) says of the Rhoads collection that it “. . . was made on the western slope of the Andes, from Guayaquil to Quito. . . .” Thus, the Orton expedition of 1867–68 crossed that portion of southern Ecuador from which *D. oreas* is well known (Fig. 8) and followed a route commonly used in the 18th and early 19th centuries. The holotype of *D. oreas* was most likely obtained en route between Guayaquil and the upper slopes of the Cordillera Occidental directly to the east. Of the localities specifically mentioned by Cope (1868) and quoted above, *D. oreas* is known from subsequent collections at Guayaquil, but Pallatanga represents the southernmost locality for *D. elegans* (Fig. 8: locality 14), from which *D. oreas* is not documented.

Apart from species recorded from Guayaquil, virtually none of Orton’s specimens from western Ecuador reported by Cope (1868) have locality data more precise than “Valley of Quito.” In a curious paradox, Orton (1871: 619) began his paper with a lengthy discussion of the importance of accurate localities and the failure of previous field workers in Ecuador (e.g., Fraser) to supply accurate specimen data: “. . . we are still very far from knowing the precise range of species. This has arisen partly from the failure of collectors to give exact localities.” Thus, although it is clear what Orton himself meant by “Valley of Quito,” that understanding does not further elucidate the geographic origin of the species described from this type locality.

## Natural History: Habitats, Seasonal Activity Patterns, Eggs, and Hatchlings

*Habitats and Seasonal Activity Patterns.* In northern Peru *Dipsas oreas* seems to be primarily an inhabitant of humid montane forests, although it occurs in secondary forest habitats if these are recent or adjacent to existing primary forests. MUSM 16750 was collected from an area of second growth at the base of Cerro Aypate (Piura department), which still had a fragment of humid forest on its crest in 1991 when the specimen was collected. Alwyn H. Gentry, who accompanied me to Cerro Aypate in 1991 classified the forest as “bmh-MT” (very humid montane forest) in the Holdridge Life Zone System (Gentry, 1995: “Cerro Aypate, Piura” in table 1). At the Río Zaña Study Site, *D. oreas* was collected from 1,450–1,800 m elevation and always inside or at the edge of primary montane humid forest. The lowest elevation constitutes the lower edge of the humid forest belt as it existed in 1987–90. Appropriate habitat at the Río Zaña Study Site occurred up to approximately 2,500 m, which might be the upper elevational extent for *D. oreas* in that local area.

During extensive field work in other areas of northern Peru, I did not encounter individuals in subhumid or arid habitats, which are common throughout the montane regions of northwestern Peru. However, a specimen from southern Ecuador was found “in a bromeliad, by day, in dry semi-deciduous thorn forest” (field notes of Linda Trueb for KU 142803). Thus, the habitat breadth of *Dipsas oreas* may be greater than suggested by my field experiences, which primarily derive from the Río Zaña Study Site. Nonetheless, all the known localities in northern Peru are areas in which fragments of humid montane forest are known to have occurred, at least historically (see *Specimens Examined and Locality Records* and Koepcke, 1961).

Wet and dry seasons at the Río Zaña

Study Site are very pronounced. Except for egg clutches found during the early dry season, I found *Dipsas oreas* only during the rainy season (approximately December or January to March or April) at the Río Zaña Study Site, although MUSM 16750 was collected 24 September 1991 at a site farther north. The contrast in activity pattern is best seen by comparing encounters during two field seasons at the Río Zaña Study Site. In nearly 2 months of continuous field work during May and June (early dry season), no *D. oreas* (except eggs) were encountered, whereas in only 2 weeks of field work from the same field camp in January (early rainy season), 10 adults and several juveniles were found. Few collecting dates accompany other specimens of *D. oreas,* but specimens have been obtained in July (KU 142803) and August (MVZ 119330). The climatic conditions that affect seasonal activity in *D. oreas* are probably very localized. The Río Zaña Study Site is the southernmost locality known for the species, and it is probably more strongly seasonal than localities farther north.

These observations suggest that *Dipsas oreas* is surface active at the Río Zaña Study Site only when ambient humidity is relatively high. During the dry season (roughly June to September), it may conceal itself in inaccessible retreats deep underground. Large boulder jumbles offering deep crevices and large surface boulders are common at the Río Zaña Study Site. Anecdotal observations (e.g., the propensity to dry out when kept in cloth bags in the field) suggest that, like some other species of *Dipsas, D. oreas* is particularly prone to desiccation (personal observations). This probably explains why no specimens were encountered during 2 months of field work during the early dry season. Temperature could also be a factor, for although average nocturnal (minimum) temperatures are only slightly higher in the rainy season compared with the dry season, the dry season was characterized by less night to night temperature equability and greater frequency of lower minimum temperatures than the wet season (see *Materials and Methods*). The rainy season also corresponds to the period when gastropod prey of *Dipsas* are most active on the surface (see next section).

*Diel Activity Patterns, Diet, and Defensive Behavior.* At the Río Zaña Study Site, *Dipsas oreas* is active nocturnally and encountered in saplings or shrubs. All active adults were found less than 2 m from the ground, and most were encountered on nights of high humidity or light rain. This species possibly never ascends to great heights in vegetation. Inactive individuals were encountered during the day on or below the surface of the ground in the following circumstances summarized from my field notes (all except MUSM 16750 from the Río Zaña Study Site).

ANSP 31779–81, 31783–86 (adult males and one adult female; see subsequent section on aggregation behavior): In well-shaded montane humid forest on the surface of leaf litter or beneath the surface litter at 1015 hr, 25 January 1989.

ANSP 31777 (adult female): Under a rock (40 cm diameter) in undisturbed montane humid forest at 1730 hr, 13 January 1989.

MUSM 5532 (near-hatchling, 178 mm SVL): Under a rock in the morning at the lower edge of the humid forest, 15 January 1989.

MUSM 16750 (adult female; Fig. 16): In a crevice in hardened lateritic soil during the day on 24 September 1991 (corresponding to the late dry season). The crevice was in a road cut in disturbed habitats at 1,950 m; it measured 2 cm wide at the ground surface, was >50 cm deep, and was covered by dead brush above. The snake was coiled about 4–5 cm below ground level and about 20 cm from the surface in a horizontal direction. The location within the crevice where the snake was found was quite dry, although it was much wetter deeper within the crevice.

In addition to these observations suggesting that *Dipsas oreas* retreats underground or under surface objects when inactive, several clutches of *D. oreas* eggs were found within a crevice in the ground at the Río Zaña Study Site (see *Eggs and Hatchlings*). On the other hand, a specimen from a dry thorn forest in southern Ecuador was found in a bromeliad (KU 142803).

Species of *Dipsas* are well known to prey upon terrestrial gastropods (e.g., Cunha and Nascimento, 1993; Martins and Oliveira, 1998; Peters, 1960a; Sazima, 1989). A single food record is available for *D. oreas* from the Río Zaña Study Site. The posterior portion of the intestine of ANSP 31777 was packed with slug and/or snail remains. Terrestrial and arboreal gastropods were both abundant and diverse at this locality during the rainy season.

*Dipsas oreas* exhibits defensive posturing common among species of Dipsadini (Cadle and Myers, 2003), including head triangulation, raising the anterior part of the body, and bringing the head and neck back into an S-shaped loop (Fig. 15). Individuals occasionally added an additional bend to the loop and the body was often "anchored" with a loose coil. Although some individuals would occasionally crawl while holding this posture, none could be induced to strike.

The posturing and head triangulation defenses of *Dipsas oreas* resemble the defensive behaviors of some vipers (Greene, 1988) and thus are potentially a form of behavioral mimicry, and perhaps the banding pattern of *D. oreas* could resemble that of some vipers to certain predators. However, vipers are said by local residents not to occur at the Río Zaña Study Site, and none were recovered in my herpetofaunal sampling there (residents report "víboras" at lower elevations toward the coast; at least one species, *Bothrops roedingeri*, potentially occurs there, although this species is documented only farther south in the Peruvian coastal region; cf. Campbell and Lamar, 2004). In other parts of the range of *D. oreas*, a possibility exists that one or more viperid species is sympatric with *D. oreas*, judging from distribution maps in Campbell and Lamar (2004); however, such sympatry remains to be demonstrated. The only venomous species potentially occurring sympatrically with *D. oreas* at the Río Zaña Study Site is *Micrurus mertensi*, which is a coastal/foothill species (Campbell and Lamar, 2004) that is recorded in my collections from 1,300 to 1,400 m at the site, just short of the lowest recorded elevation for *D. oreas* (1,450 m). However, there is (to my perception) no particular resemblance between these two species.

*Comparisons of Behavior with Other Species of* Dipsas. Species of *Dipsas* occur in tropical dry forests and rain forests from central Mexico to the subtropical zone of southern Brazil, thus inhabiting an array of relatively aseasonal to highly seasonal environments. As indicated for the Río Zaña Study Site, seasonal activity correlated with the onset of rains or high ambient humidity has been reported in other species of *Dipsas* inhabiting seasonal environments. For example, Hartmann et al. (2002) found that adult *D. albifrons* were active only during the rainy season in the Atlantic forest of southeastern Brazil (juveniles seemed less seasonal in their activity). On the other hand, a related snake from the same region, *Sibynomorphus neuwiedi*, is more active during the cooler, drier season (Marques et al., 2001). Activity patterns of species of *Dipsas* from less seasonal rain forests in equatorial Amazonia do not show strong seasonality (e.g., Martins and Oliveira, 1998).

Cadle and Chuna (1995: footnote 5) commented on the seemingly paradoxical behavior of an arboreal snake such as *Dipsas oreas* retreating to the ground surface or subsurface during its inactive period, rather than seeking arboreal retreats. However, this behavior could be frequent in both montane and lowland members of the genus, as the following remarks indicate for several species.

*Dipsas catesbyi*: At La Selva Lodge (Río Napo, Ecuador) I found an adult *Dipsas catesbyi* (not collected) under dead leaves in deeply shaded forest at 1500 hr. At the same locality another individual encountered while active in low vegetation at night dropped to the ground after several minutes of observation and hid underneath the leaf litter. Comments associated with other specimens include "on ground at night" (FMNH 165846; Colombia, Putumayo department) and "Under banana leaves on ground [presumably during the day] (FMNH 39640; Peru, Ayacucho department).

*Dipsas indica*: FMNH 165847 (Colombia, Putumayo department) was "on ground at daytime" (remarks in FMNH catalogue entry).

*Dipsas latifasciata*: LSUMZ 45499 (Peru, Pasco department) was "caught on ground of second growth at edge of humid forest in late afternoon." (remarks on field tag).

*Dipsas peruana*: USNM 299232–34, MUSM-JEC 6750 (Peru, Puno department). I collected these specimens inactive under rocks during the day. This locality was a somewhat dry rain shadow valley with xerophytic vegetation and few epiphytes to create arboreal retreats.

Observations of terrestrial activity for other species of *Dipsas* seem rarely to have been reported. Duellman (1978) reported terrestrial and arboreal activity for *D. catesbyi* in Ecuador. Orcés and Almendáriz (1987) reported, without stating whether the snakes were active or inactive, that neither *D. ellipsifera* nor *D. elegans* seemed to be arboreal snakes. At least one species, *D. pavonina* in central Amazonia, may be primarily terrestrial when foraging at night (Martins and Oliveira, 1998), although Duellman (1978: 240) reported arboreal activity for this species in western Amazonia. These examples suggest that diel movement between terrestrial retreats and arboreal microhabitats when nocturnally active may be common behaviors in some species of *Dipsas,* at least at some localities. Other species may even be terrestrial while active.[6] Conversely, many diurnal terrestrial snakes ascend vegetation to sleep at night, perhaps in response to carnivorous ants (Martins, 1993). At the Río Zaña Study Site, ants did not seem especially prevalent compared with my experience in lowland Amazonian rain forests; diurnal colubrids of genera known elsewhere to sleep in vegetation were never encountered sleeping in vegetation at the Río Zaña Study Site (e.g., *Chironius, Dendrophidion, Leptophis,* and *Mastigodryas*).

The factors that might affect where a snake seeks refuge during its inactive period are numerous, and individual, seasonal, geographic, and species-specific patterns of behavior are possible. Geographic trends may be related to the availability of arboreal retreats such as epiphytes—epiphytes are much more abundant in continually wet tropical rain forests than in more seasonal or subhumid forests (e.g., Myers, 1969). Bromeliads and other epiphytes are common at the Río Zaña Study Site, so the propensity for *Dipsas oreas* at that site to use terrestrial retreats when inactive is not because of the lack of appropriate arboreal ones. Bromeliads were routinely searched at the Río Zaña Study Site but yielded only frogs (*Eleutherodactylus* and *Gastrotheca*), and these only during the rainy season. The extended dry season at the Río Zaña Study Site results in low ambient moisture and humidity within the forest, and the surface of the soil, the leaf litter, and even many bromeliads become very dry. During the dry season, some streams at the Río Zaña Study Site temporarily cease flow, and the humidity is low enough that desiccation becomes a problem for the aerial egg clutches of centrolenid frogs laid toward the end of the rainy season (Cadle and McDiarmid, 1990). The factors combined probably explain the terrestrial seclusion behavior at this locality for *D. oreas.*

Although the observations reported here suggest that terrestrial seclusion for several species of *Dipsas* occurs with some frequency, other observations suggest that arboreal seclusion also occurs within *Dipsas.* Porto and Fernandes (1996) reported an inactive *D. neivai* found within a bromeliad on a tree branch close to the ground, and I collected an inactive *D. vermiculata* (MVZ 163259) from a bromeliad 2 m from the ground during the day. Parker (1926) reported that the type of *D. variegata trinitatis* was obtained from a bromeliad on a fallen tree. Charles W. Myers collected several inactive *D. temporalis* from bromeliads on the sides of trees 1.2–3 m aboveground during the day (Cadle and Myers, 2003: 36).

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[6] Movement between terrestrial retreats and arboreal active sites may be more widespread in tropical nocturnal, arboreal snakes than is currently recognized. In Madagascar, the colubrids *Geodipsas laphystia* and *G. zeny* are similar to species of *Dipsas,* in being nocturnally active in low vegetation (Cadle, 1996). However, both species are occasionally found hidden in moist leaf litter on the ground during the day (personal observations).

*Eggs and Hatchlings.* Cadle and Chuna (1995: 32–34) reported communal egg-laying in *Dipsas oreas* (21 total eggs), which in that instance was coincident with a large number of communally laid eggs of the gymnophthalmid lizard, *Macropholidus ruthveni.* The eggs, discovered 17 June 1987 at the lower edge of the humid forest (1,490 m) at the Río Zaña Study Site, were underground in a moist crevice within a road embankment. The eggs were 20–30 cm from the entrance to the crevice and 15 cm beneath the surface of the soil (the crevice ran somewhat parallel to the soil surface); dimensions of the *Dipsas* eggs were 28–30 × 20 mm. On the basis of their clustering within the crevice, the snake eggs probably represented three clutches of eight, seven, and six eggs. One egg was opened at the time from each of the two deepest clutches and contained advanced embryos of slightly different stages. Five of the eggs were transported in plastic bags containing moist paper towels back to an air-conditioned office, where they were kept in similar fashion on a table. These eggs hatched between 23 September and 1 October. Hatchlings (FMNH 232570–72, MUSM 16751–52) were 214–225 mm total length (172–176 mm SVL) and 2.8–3.2 g. A hatchling from this clutch is illustrated in Figure 17, and another was illustrated by Cadle and Myers (2003: fig. 11).

Two hatchlings or near-hatchlings of *Dipsas oreas* (MUSM 5530, 5532; total lengths 230–243 mm) were collected 13–15 January 1989 near the site where the above eggs were discovered. It seems likely that these hatchlings derived from eggs laid the previous dry season, as indicated by the eggs discovered in June and their slightly larger size than the above series of hatchlings.

Two other females of *Dipsas oreas* from Ecuador were gravid, and clutch sizes were estimated by palpation through the ventral body wall. ANSP 18117 (421 mm SVL) contained four eggs. BMNH 60.6.16.56 (566 mm SVL) contained about 8 eggs. No collection dates are available for these specimens.

## Aggregation Behavior in *Dipsas oreas*

A peculiar aggregation of *Dipsas oreas* was discovered on 25 January 1989 at 1,800 m at the Río Zaña Study Site. At 10:15 a.m., a field assistant found a ball of four snakes on the surface of the leaf litter adjacent to a small log (10–15 cm diameter, 2.5 m long) in a somewhat disturbed patch of cloud forest; all of these snakes were intertwined in a tight ball. Another individual was on the leaf litter surface about 20 cm from the ball. After alerting me to the discovery we returned to the site and found another snake hidden under the leaf litter (15–20 cm deep) where the initial ball was found. At the opposite end of the log (2.5 m from the ball), another individual was hidden under the leaf litter. A search of the immediate area (surface and under logs, litter, etc.) turned up no more snakes. The night before finding the aggregation included a light drizzle for several hours; on the morning of the encounter, the leaf litter was wet and the day was overcast. Temperature at 11:00 a.m. was 15° C.

All snakes were quiescent and loosely or tightly coiled. The four snakes in the initial ball were completely and tightly intertwined, and consisted of an adult female and three adult males. The three individuals not associated directly with the ball were adult males. The female is ANSP

31784 and the males are ANSP 31779–81, 31783, 31785–86 (497–551 mm SVL; see Figs. 18, 19).

Aggregations of snakes occur for a variety of reasons, including hibernation (in temperate snakes), response to unfavorable temperature or humidity conditions, feeding, mating, and oviposition (e.g., Amr et al., 1997; Ford and Burghardt, 1993: 139–140; Gillingham, 1987: 197–198; Gregory et al., 1987: 370–373; Halpern, 1992; Noble and Clausen, 1936). The aggregation of *Dipsas oreas* just described seems unlikely to be due to unfavorable environmental conditions, hibernation, or feeding. The rainy season at the Río Zaña Study Sites commences in December or early January (as in 1989) and corresponds to the most active and environmentally favorable period for *D. oreas* and its gastropod prey. On the other hand, several observations suggest an association with reproductive behavior for the aggregation: all individuals are adults and all except one are males. This suggests that the aggregation may have been for mating, as does the morphology of the reproductive tracts described below. Unfortunately, the aggregation was disrupted before specific behaviors such as copulation or combat could be assessed. The fact that the aggregation was discovered during the day in a snake typically nocturnally active prompts questions that only additional serendipitous field observations could answer: Was this aggregation simply a continuation of courtship activity that had begun the previous night? Alternatively, do males locate females during the day?

Gregory et al. (1987: 370) defined aggregations as "any concentration of snakes in a relatively small area such that the density of snakes in the aggregation contrasts sharply with that in the surrounding area." Thus, aggregations need not involve continuous physical contact among individuals. In some snakes, males in mating aggregations are not necessarily continuously associated with the female, such as three of the males in the aggregation of *Dipsas oreas* just described. For example, Feio et al. (1999) observed six male *Chironius flavolineatus* courting a female, but only two were ever directly associated with the female, the other males being nearby on the ground or low bushes. Thus, even though three males were not directly associated with the tight cluster of *D. oreas,* it seems very unlikely that they were only coincidentally close by.

That the aggregation of *Dipsas oreas* described was associated with reproduction is also suggested by the morphology of the reproductive tracts of the female and males. The female (ANSP 31784) has small ovarian eggs (2–4 mm) in her left ovary. These are somewhat yellowish, perhaps indicating the initiation of yolk supply to the ova. Her left oviduct is extremely dilated (3.5–4 mm broad and thrown into many pleats), which is the condition observed in female snakes of many species prior to ovulation and fertilization (review in Fox, 1977). The middle portion and cranial end of the left oviduct, corresponding to the tube portion of the oviduct (Guillette et al., 1989), are particularly dilated and pleated. The right oviduct is less dilated than the left and not at all pleated. Except for a single ovum similar in size to those in the left oviduct, eggs in the right ovary are smaller and paler than those in the left ovary. These observations suggest that the left reproductive tract of the female was gearing up for reproduction. Moreover, the size of the ova in the left ovary correspond to follicle size classes II ("early growth") to III ("hydration and initial vitellogenesis") recognized for *D. catesbyi* by Zug et al. (1979: 2–3), which corroborates the other indications of reproductive competence of this female. The males in the aggregation have swollen and highly convoluted vasa deferentia, which are characteristic of male snakes during the breeding season.

Because so little is known of reproductive cycles and behavior of tropical snakes, it is worth exploring the details known for *Dipsas oreas* at the Río Zaña Study Site and attempting to paint a scenario of what seems to occur. At the Río Zaña site, eggs of *D. oreas* with well developed embryos were discovered in mid-June in a well-secluded, relatively cool location deep within a crevice (details reported above). The advanced developmental stages of two embryos suggest that the eggs were laid some time prior to their discovery in mid-June. This observation, combined with the observed aggregation of several adult males and an adult female in late January, suggests that a mating period in late January may not be unreasonable. Moreover, the condition of the oviducts in the female and the vasa deferentia in the males suggest that these individuals were reproductively competent. The delay between the presumed mating period and egg laying would give ample time for fertilization and yolking of the ova.

In a related colubrid, *Sibynomorphus ventrimaculatus,* mating apparently takes place several months (perhaps as many as seven) before vitellogenesis commences and egg-laying occurs (Cechin and Oliveira, 2003). A similar sequence in *Dipsas oreas* would explain the small follicles in the female described above well before the inferred oviposition season. The strong seasonal activity pattern of *D. oreas* at the Río Zaña Study Site, as well as the few observations on eggs and hatchings, imply that reproduction is strongly seasonal in this species, at least in the southern part of its range. Other species of *Dipsas* that inhabit less seasonal environments of Amazonia or the Atlantic Forest of southeastern Brazil are apparently aseasonal in their reproductive patterns (Zug et al. [1979] for *D. catesbyi*; Porto and Fernandes [1996] for *D. neivai*), and some other members of the Dipsadini have extended periods of oviposition (e.g., two species of *Sibynomorphus*; Laporta-Ferreira et al., 1986).

Aggregation behavior is best known in north temperate species of natricine colubrids and viperids, although scattered observations of scolecophidians, elapids, and other groups of colubrids suggest that aggregation behavior is taxonomically widespread. Aggregations have previously been reported in three other species of Neotropical colubrids. An aggregation of *Rhadinaea calligaster* (Myers, 1974: 221) in a pile of decomposing thatch consisted of six females and a male. Females were apparently attracted to the site for oviposition because a communal nest was in the same pile of debris. The other cases involve aggregations for mating functions in snakes of the clade Colubrinae (*sensu* Cadle, 1984c, 1985): *Drymobius margaritiferus* (Campbell, 1998: 213) and *Chironius flavolineatus* (Feio et al., 1999). The observations reported here for *Dipsas oreas* constitute the first report of aggregation behavior in any species of Dipsadini (*Dipsas, Sibon, Tropidodipsas, Sibynomorphus*) and one of only three cases of mating aggregations in Neotropical colubrids. Because communal nests are now known in two distantly related members of the larger Neotropical clade Dipsadinae (*sensu* Cadle, 1984b; Zaher, 1999), *D. oreas* and *Rhadinaea calligaster,* aggregation behavior for oviposition may be widespread within this group if particular oviposition sites offer favorable conditions for egg development.

## TAXONOMIC AND GEOGRAPHICAL NOTES ON *DIPSAS GRACILIS, D. LATIFASCIATUS,* AND *D. LATIFRONTALIS*

While studying the systematics of species in the *Dipsas oreas* complex and others in western Ecuador and Peru (e.g., Cadle and Myers, 2003) I had occasion to examine specimens of other species reported from the eastern and western versants of the Andes in this region. In a few cases, the specimens examined amplified distributional knowledge of species or raised questions concerning systematic and nomenclatural issues. I here comment on these points for three species. *Dipsas gracilis* has been well known from the western lowlands of Ecuador, but new information extends its range into Peru. *Dipsas latifasciatus* and *D. latifrontalis* have been reported from eastern Ecuador and/or Peru, but my examination of specimens disclosed some systematic and nomenclatural problems relative to the treatment of these species in the literature. Detailed locality data on specimens of these taxa I examined are given in the *Specimens Examined and Locality Records*. See *Note Added in Proof*, p. 136.

### Dipsas gracilis

*Dipsas gracilis* (Boulenger, 1902) was not recorded south of Guayaquil, Ecuador (Peters, 1960a) until Tello (1998) reported it from a lowland (620 m) evergreen rain forest in extreme northwestern Peru on the basis of MUSM 17589 (Quebrada de los Naranjos, Tumbes department). I provisionally refer two additional specimens from northern Peru to *D. gracilis*, MUSM 2700–01 (Río Quiroz valley, Piura department). Although *D. gracilis* thus far has been reported in detail only from western Ecuador (Peters, 1960a; Peters and Orejas-Miranda, 1970), Perez-Santos and Moreno (1988, 1991) reported the species from Colombia without providing documentation. A specimen of *Dipsas* that I examined from northwestern Colombia near the Panama border (FMNH 74376) had been previously identified as *D. gracilis*, but I tentatively refer this specimen to *D. viguieri*; see comments in the following section (key to species) concerning some difficulties in distinguishing *D. gracilis* and *D. viguieri*. I here comment on characteristics of the Peruvian specimens of *D. gracilis*, whose scutellation and other characters are summarized in Table 4. Unfortunately, my examination of MUSM 17589 was brief, and basic data were not completed, although the specimen is well preserved. All three Peruvian specimens are males, so the most relevant comparison would be males of Ecuadorian *D. gracilis* (Table 4).

MUSM 17589 was obtained during a biological inventory of the lowland tropical forests of Tumbes department (Wust, 1998a). It is an adult male in excellent condition with well-everted hemipenes. The specimen has 22 broad black bands (encompassing 6–8 dorsal scale rows) that extend completely across the venter. Interspaces are whitish (3–4 dorsal rows in breadth) with brownish stippling concentrated in the central part of each interspace. The head is white with many irregular black markings on the top and sides.

Quebrada de los Naranjos, whence MUSM 17589 comes, is within a region of lowland humid tropical forest extending southward from Ecuador into far northwestern Peru (Chapman, 1926; Koepcke, 1961). This forest is the only truly lowland humid forest in western Peru and has never been extensive; remaining fragments are now a protected reserve (Wust, 1998a). Tello (1998:79) described the vegetation of Quebrada de los Naranjos as "an ephemeral thicket composed mostly of small plants of the Rubiaceae and ferns." Wust (1998b:22) stated that "In the hills of Quebrada de los Naranjos the forest is humid and evergreen, reaching more than 20 m in some parts, and with a more or less uniform canopy dominated by [*Ficus, Centrolobium, Vitex, Pouteria, Ocotea, Bombax*, and *Gallesia*]."

MUSM 2700–01 are assigned only provisionally to *Dipsas gracilis* because they are in poor condition (soft, poorly preserved, and with pattern elements obscure). The MUSM catalogues indicate that the specimens were collected 17 March 1966 (collector not listed) from the imprecise locality "Valle del Río Quiroz." Additional geographical indications in the catalogue (perhaps added later when the specimens were catalogued in Lima) include "Piura [department], Pv. [Provincia] Ayabaca." The Río Quiroz flows northwestward across extreme northern Piura department (western versant of the Andes) north of the Cordillera Guamani and eventually joins the Río Chira, which drains the southern part of Loja Province, Ecuador. Ayabaca Province is at the northern extremity of Piura department on the Ec-

TABLE 4. STANDARD CHARACTERS FOR PERUVIAN SPECIMENS REFERRED TO *DIPSAS GRACILIS* COMPARED WITH A SAMPLE FROM ECUADOR. HEAD SCALES ARE SCORED AS INDICATED IN TABLE 1. BILATERAL COUNTS ARE SEPARATED BY A SOLIDUS (LEFT/RIGHT). $N$ = NUMBER OF SPECIMENS OR OBSERVATIONS; SVL = SNOUT TO VENT LENGTH.

| | MUSM 2700 male | MUSM 2701 male | MUSM 17589 male | *Dipsas gracilis* Ecuador |
|---|---|---|---|---|
| Total length (SVL) (mm) | | | | |
| Largest male | 665 (471) | 375 (275) | — | 760 (524) |
| Largest female | | | | 727 (515) |
| Tail length/total length | | | | |
| Male | 0.29 | 0.27 | — | 0.30–0.33<br>0.32 ± 0.01 ($N = 6$) |
| Female | | | | 0.29–0.31<br>0.30 ± 0.01 ($N = 3$) |
| Maxillary teeth | 18 | — | — | 17 ($N = 1$)<br>19 ($N = 1$)<br>24 ($N = 2$) |
| Dorsal scales | 15-15-15 | 15-15-15 | 15-15-15 | 15-15-15 |
| Ventrals (and preventrals) | | | | |
| Male | 187 (2 preventrals) | 189 (1 preventral) | 192 (1 preventral) | 199–210 (1–5 preventrals)<br>203.8 ± 3.97 ($N = 6$) |
| Female | — | — | — | 194–199 (2–4 preventrals)<br>196.0 ± 2.65 ($N = 3$) |
| Subcaudals | | | | |
| Male | 104 | 109 | 94 | 114–128<br>120.7 ± 5.92 ($N = 6$) |
| Female | — | — | — | 105–117<br>109.0 ± 6.93 ($N = 3$) |
| Total segmental counts | | | | |
| Male | 291 | 298 | 286 | 313–333 ($N = 6$) |
| Female | — | — | — | 298–316 ($N = 3$) |
| Anal scale | Single | Single | Single | Single |
| Loreal pattern | 1 | 1 | — | 2 ($N = 18$) |
| Preoculars | 1/1 | 1/1 | — | 0 ($N = 18$) |
| Postoculars | 2/2 | 2/2 | — | 2 ($N = 4$)<br>3 ($N = 14$) |
| Primary temporals | 2/2 | 2/1 | — | 1 ($N = 1$)<br>2 ($N = 15$)<br>3 ($N = 2$) |
| Secondary temporals | 3/3 | 2/2 | — | 2 ($N = 11$)<br>3 ($N = 7$) |

Table 4. Continued.

| | MUSM 2700 male | MUSM 2701 male | MUSM 17589 male | *Dipsas gracilis* Ecuador |
|---|---|---|---|---|
| Tertiary temporals | 4/3 | 3/3 | — | 0 (*N* = 2)<br>3 (*N* = 14)<br>4 (*N* = 2) |
| Supralabials (touching eye) | 11 (5–7)/11 (5–7) | 10 (4–6)/11 (4–7) | — | 8 (3–5) *N* = 1<br>9 (3–5) *N* = 3<br>9 (4–5) *N* = 4<br>9 (4–6) *N* = 2<br>10 (3–5) *N* = 1<br>10 (4–6) *N* = 7 |
| Infralabials | 13/13 | 13/13 | — | 10 (*N* = 1)<br>11 (*N* = 3)<br>12 (*N* = 8)<br>13 (*N* = 4) |
| Number of infralabials in contact behind mental | 1 pair | 2 pairs | 1 pair | 1 pair (*N* = 9) |
| Number of bands or blotches on body | 24 | 21 | 22 | 13–19 (*N* = 9) |

uadorian border. The general region is arid in lower reaches of the valley to the west and subhumid toward the east. Relictual patches of humid forest still existed in the 1990s at higher elevations in montane regions in the eastern part of the valley (personal observations; see above notes on habitats of *D. oreas* in northern Peru). *Dipsas gracilis* is otherwise known only from the lowlands (<1,000 m), whereas the only parts of the Río Quiroz valley presently having humid forest habitats are at higher elevations in the eastern part of the river system (>2,000 m).

The pattern elements visible in MUSM 2700–01 are similar to other specimens of *Dipsas gracilis*. The dorsal pattern consists of a series of dorsal blotches or bands, which, when viewed in lateral aspect, are oval on the anterior body and round posteriorly. The anterior bands nearly meet midventrally; posterior ones encroach onto the outer edges of ventrals. The top of the head is mainly dark blackish with light patches and flecks (more light patches are present in the smaller specimen, MUSM 2701). The vertebral scale row is greatly expanded (1.5–2× the width of the paravertebral rows).

The three Peruvian specimens referred to *Dipsas gracilis* conform generally to other males of *D. gracilis* I examined, but there are differences from Ecuadorian specimens as well (Table 4). The Peruvian specimens have lower ventral (187–192) and subcaudal (94–109) counts than males from Ecuador (ventrals 199–210, subcaudals 114–128). MUSM 2700–01 have shorter tails and a different loreal pattern from Ecuadorian specimens. In *D. gracilis* from Ecuador, all the dorsal bands are complete across the venter (anterior body) or encroach very broadly onto the ventral scutes, nearly meeting midventrally (posterior body). This is the case in MUSM 17589, but in MUSM 2700–01, the posterior bands end on the outer edges of the ventral scutes.

Although some scutellation characteristics of the three Peruvian specimens referred to *Dipsas gracilis* are outside the range of scale counts seen in Ecuadorian specimens of *D. gracilis,* they are likewise dissimilar to other species of *Dipsas* known from western South America in scutellation and/or color pattern. *Dipsas oreas* is also known from the "valley of the Río Quiroz" (Fig. 16, Fig. 23: locality 7), the locality for MUSM 2700–01. However, compared with characters of *D. oreas* males (Table 1 for total sample, Table 3 for Peruvian populations), MUSM 2700–01 have significantly greater numbers of ventrals, subcaudals, and supralabials. Moreover, the number of maxillary teeth of MUSM 2700 (18) is much greater than the number in a large sample of *D. oreas* (12–14; Table 1). Collection of additional material might permit a resolution of the systematic status of these Peruvian populations, particularly if new specimens of *D. gracilis* from the geographic gap between northern Peru and the vicinity of Guayaquil, Ecuador, can be obtained. Biogeographically, the presence of *Dipsas gracilis* in lowland humid forests of Tumbes department (MUSM 17589) was perhaps expected on the basis of other geographic and biological data from this region (e.g., Chapman, 1926; Koepcke, 1961), and MUSM 17589 is well documented in the context of a biological inventory (Wust, 1998a).

On the other hand, MUSM 2700–01 are more problematic because they are not accompanied by specific locality data or collector, and there may be reason to question their origin. Appropriate habitats do not apparently exist presently in the lowlands of the Río Quiroz valley, and *Dipsas gracilis* is otherwise known only from lowland localities. Moreover, *D. latifasciata* is recorded from inter-Andean valleys immediately east of the Río Quiroz (e.g., by MCZ 17404; see comments below). Most characteristics of the color pattern, scale counts, body proportions, loreal scale pattern, and maxillary tooth counts of MUSM 2700–01 are similar to those I recorded for *D. latifasciata* from the Amazonian versant of Peru and Ecuador (unpublished data). One characteristic of the patterns of MUSM 2700–01 is more typical of *D. latifasciata* than of *D. gracilis*: The posterior bands fail to encroach broadly onto the ventral scutes or to meet midventrally. If, in fact, MUSM 2700–01 were obtained from east of the continental divide or if *D. latifasciata* occurs on both versants of the Andes in this region, then the identity of these specimens should be reconsidered.

## *Dipsas latifasciatus* and *D. latifrontalis* in Eastern Ecuador and Peru

*Dipsas latifasciata* (Boulenger, 1913) was described from the type locality "Upper Marañon, eastern Peru," and *D. latifrontalis* (Boulenger, 1905) has the type locality "Aricaqua" [Venezuela]; Peters (1960a: 110) identified the latter locality as the town of that name on the Amazonian slopes of the Andes in western Venezuela south of Mérida. These names and their applicability to populations in eastern Ecuador require further study. Without examining the holotype of either species, Peters (1960a) assigned specimens from eastern Ecuador to each. However, Peters' (1960a) characterizations reveal similar scutellation and few distinctions between them, such as whether some or none of the dorsal bands fail to meet midventrally, as stated in Peters' key (1960a: 33, couplet 35) or by the number of infralabial pairs in contact behind the mental. The last character is now known to be highly variable within species of *Dipsas*; for examples, see descriptions of the three species discussed in detail in this report or Cadle and Myers (2003) for *D. nicholsi* and *D. andiana.* There is broad overlap in the scutellation characters of these two taxa as construed by Peters (1960a). This in itself is not necessarily grounds for questioning their validity, but in combination with the other similarities noted by Peters and some inconsistencies in his own discussions (see below), it begs the question of how these nominal taxa are distinguished and how the names should apply to Ecuadorian and Peruvian specimens.

Moreover, Peters (1960a) had little material of each species, particularly from near the type localities. He referred only three specimens from extreme southern Ecuador and northern Peru to *D. latifasciata.* More problematic was his referral of only one specimen from Venezuela to *D. latifrontalis* but, in addition, 44 others from eastern Ecuador. Thus, the distribution of *"Dipsas latifrontalis,"* as Peters (1960a: 99) conceived it, left a broad gap across eastern Colombia, from which no specimens referred to either of these species were reported. Peters himself seems to take great pains to justify his applications of these names to samples available to him based only on the type descriptions. Similarly, he justified his referral of the names *Leptognathus palmeri* Boulenger (1912) (type locality, "El Topo, Río Pastaza, Ecuador") and *L. praeornata* Werner (1909) (type locality, "Venezuela") to the synonymy of *Dipsas latifrontalis* by extended discussion of relatively few characters in the original descriptions (Peters, 1960a: 103, 109–110). The brevity of the original descriptions of all these taxa and the poor comprehension of intraspecific variability within *Dipsas* at the time of their descriptions mean that reference to the types is needed to resolve the systematics of these snakes.

These peculiarities and my interpretations of some material that both Peters and I examined lead me to question the proper name of specimens from eastern Ecuador and Peru. MCZ 17404, a specimen that Peters (1960a) assigned to *D. latifasciata,* has the pattern by which he characterized *D. latifrontalis* (all bands fail to meet midventrally). In fact, Peters (1960a: 103) stated that this specimen was "intermediate in some characters between what might be called typical *latifrontalis* and *latifasciata*. . . ." In three specimens that Peters assigned to *D. latifrontalis* from the same general area of Ecuador ("Llanganates Area" [probably southwestern Napo Province]), two (FMNH 23530–31) show the pattern characteristic ascribed to *D. latifrontalis,* whereas FMNH 23532, although it has a predominantly black venter, seems to have bands meeting midventrally, the pattern that Peters ascribed to *D. latifasciata.* Peters (1960a: 103) suggested the possibility that additional collections might "demonstrate that the relationship between [*latifrontalis* and *latifasciata*] is at best on the subspecific level."

Interpretive problems such as these suggest that a new look at snakes with the requisite characteristics from Venezuela, Ecuador, and Peru is warranted. As with many similar problems concerning species identities in *Dipsas,* adequate resolution will require renewed study of the types and other geographically proximate specimens. Consequently, Peters' assignment of specimens from eastern Ecuador to *D. latifrontalis* is unconvincing, as is his suggestion of a possible subspecific relationship between *D. latifrontalis* and *D. latifasciatus.* The specimens here referred to *D. latifasciata* (see *Specimens Examined and Locality Records*) are done so provisionally, pending further study of the Ecuadorian, Peruvian, and Venezuelan material (including types) referred to *D. latifasciata* and *D. latifrontalis.* Full resolution of the systematics of this group should also review the validity and proper synonymy of the names *Leptognathus palmeri* Boulenger (1912) and *L. praeornata* Werner (1909), which Peters considered synonyms of *D. latifrontalis* on the basis solely of the type descriptions.

## KEY TO SPECIES OF *DIPSAS* IN WESTERN SOUTH AMERICA

I provide the following key to assist in identifying species and individual specimens of *Dipsas* in western South America. Six species of *Dipsas* are known from the western slopes of the Cordillera Occidental and adjacent Pacific lowlands of Ecuador and Peru: *D. andiana, D. elegans, D. ellipsifera, D. gracilis, D. oreas,* and *D.*

*temporalis.* All of these are known from Ecuador, but only *D. oreas* and *D. gracilis* have been reported from Peru. The key also includes three additional species known or expected in the Chocó region of Colombia: *Dipsas sanctijohannis, D. viguieri,* and (possibly) *D. nicholsi*; the last species, previously known only from central Panama (Cadle and Myers, 2003), has recently been recorded in eastern Panama near the Colombian border (Myers et al., unpublished data). Characters of *D. nicholsi* and *D. andiana* in the key are based on diagnoses given in Cadle and Myers (2003) and another female of *D. nicholsi* reported by Myers et al. (ms.). The differential characteristics of *D. sanctijohannis* in the key are based on data from Peters (1960a) and on data kindly provided by Charles W. Myers from specimens he examined. Characters of all other species are based on discussions in this paper (*D. elegans, D. ellipsifera, D. gracilis, D. oreas*) or unpublished data (*D. temporalis*) in conjunction with some data from Peters (1960a).

Without additional study, I am unable to adequately differentiate *Dipsas viguieri* (eastern Panama and northern Chocó, Colombia) and *D. gracilis* (western Ecuador and extreme northern Peru). Geography currently seems to be the only reliable means of assigning names to specimens of these species. The characters that Peters (1960a) used to distinguish *D. viguieri* and *D. gracilis* (e.g., preocular presence/absence, number of postoculars) are known to be highly variable intraspecifically within *Dipsas.* Peters (1960a: 52) considered the two perhaps only "subspecifically distinct" and otherwise noted (Peters, 1960a: 48) that "The characters separating [*Dipsas gracilis*] and *D. viguieri* are comparatively weak ones. . . ." Thus, specimens of *D. viguieri* will key out to *D. gracilis* with this key. The differential characters (if any) of these two species and the disjunction (or lack thereof) between their ranges in western Colombia require further research. Nonetheless, if these two taxa are closely related or conspecific, then they would add a third example within *Dipsas* of a biogeographic connection between northwestern (Chocoan) South America and eastern Panama. The other examples are *D. andiana–D. nicholsi* (Cadle and Myers, 2003) and *D. temporalis,* which has scattered records from northwestern Ecuador into eastern Panama.

In addition to illustrations provided herein, illustrations and discussions of some of the relevant taxa are found in Peters (1960a; *D. gracilis,* pl. Ib, c and *D. ellipsifera,* pl. IVa), Kofron (1982; *D. elegans, D. ellipsifera,* and *D. oreas*), and Cadle and Myers (2003; *D. andiana, D. nicholsi,* and *D. oreas*). The key is dichotomous except for the last numbered section, a triplet.

1. Dorsal bands very broad anteriorly and posteriorly, covering 8 or more dorsal scale rows in longitudinal dimension; bands continuous, or nearly so, across the venter at least anteriorly. Subcaudals $>90$, often $>100$ (up to 132). Tail $\geq 29\%$ of total length. Either no infralabials in contact behind the mental scale, or one pair in contact .................... 2

– Dorsal bands narrower, covering 10 or fewer dorsal scale rows in longitudinal dimension (usually $<7$); anterior bands usually much broader than posterior bands, and all bands end on outer edges of ventrals or on lowermost dorsal rows. Subcaudal counts variable, but usually $<100$ (except male *D. andiana,* up to 106). Tail $\leq 28\%$ of total length. At least one pair of infralabials in contact behind the mental scale .................... 3

2. No infralabials in contact behind the mental scale. Anterior pair of chin shields very small (in contact with mental), followed by a pair of much larger chin shields. .................... *Dipsas temporalis* (Werner) (eastern Panama, western [Chocoan] Colombia, and western Ecuador; primarily in low uplands in Panama, 800–1,000 m; apparently also in the lowlands in Colombia and Ecuador)

– One pair of infralabials in contact behind the mental scale. Anterior pair of chin shields about the same size as, or only slightly smaller than, the second pair. .................... *Dipsas gracilis* (Boulenger) (lowlands [150–620 m] of western Ecuador from just north of the equator to extreme northwestern Peru [Tumbes and, less certainly, Piura departments; see discussion herein]) [*D. viguieri* will also key here]

3. A distinct V- or U-shaped mark with well-defined, regular borders on top of the head (apex anteriorly at frontal/prefrontal border); head otherwise pale brown or grayish brown and relatively unmarked. Ventrals ≥185 in males and females. Subcaudals >90 in males, ≥82 in females. .................... 4

– No distinct stereotypic inverted V- or U-shaped mark on the top of the head.[7] Head usually with many dark markings, including darkened suture lines; entire head may be dark. Ventrals <190 in males and females. Subcaudal counts variable, but often much less than 80 .................... 5

4. Ventrals 185–196 in males, 185–191 in females. Subcaudals 91–106 in males, 82–83 in females. Branches of the V-shaped mark on top of head generally not connected to the first pair of neck blotches. Dorsal blotches at midbody taller than wide. .................... *Dipsas andiana* (Boulenger) (lowlands and lower montane slopes of western Ecuador from approximately the equator to latitude 2°S; 5–1,140 m)

– Ventrals 198–208 in males, 200–206 in two females. Subcaudals 92–98 in males, 87–95 in females. Branches of the V-shaped mark on top of head connected to the first pair of neck blotches. Dorsal blotches at midbody wider than tall. .... *Dipsas nicholsi* (Dunn) (lowlands <200 m in the Río Chagres basin of central Panama; Darién highlands, 875 m, of extreme eastern Panama; Myers et al., ms.)

5. Ventrals 153–164 in males, 157–158 in two females. Subcaudals 72–78 in males, 62–63 in two females .... *Dipsas ellipsifera* (Boulenger) (known only from the valley of the Río Mira in extreme northwestern Ecuador, 570–2,600 m)

– Ventrals >165 in males and females. Subcaudals >80 in males, >70 in females .................... 6

6. Subcaudals 82–91 in males, 70–83 in females. Top of head usually with a pair of large elongate irregular blotches centered on the parietal region. Head otherwise with many dark spots and flecks and darkened suture lines. Thirty or fewer bands on the body, with anterior bands covering more than 5 dorsal rows in longitudinal dimension. Each band in adults usually with a somewhat pale central portion, but bands in most specimens without distinct borders enclosing a highly contrasting pale central area. Anterior bands end on outer edges of ventrals. Venter dirty whitish to grayish, usually with many small dark irregular spots and streaks .................... *Dipsas oreas* (Cope) (western Ecuador and northwestern Peru, approximately latitude 2°S to nearly 7°S; primarily Andean foothills and slopes, 1,400–2,600 m; lowlands in the vicinity of Guayaquil, Ecuador)

– Subcaudals 94–105 in males, 68–88 in females. Top of head with many dark brown irregular marks on a pale brown ground color, but generally not forming paired irregular blotches and occasionally nearly solid dark brown. Twenty-five to 46 bands on body. Each band in adults comprising a pair of bold blackish vertical edges enclosing a contrasting pale brown central portion. Anterior bands cover no more than 5 dorsal scale rows and end on outer edges of ventrals. Venter grayish with many small dark flecks and squarish markings, which sometimes form longitudinal arrays .................... *Dipsas elegans* (Boulenger) (western Ecuador from just north of the equator to approximately latitude 1°10′S, 500–2,650 m)

– Subcaudals 86–94 in males, 70–83 in females. Top of head in adults relatively uniform medium brown (dark-spotted in juveniles). Twenty-one to 28 bands on body; anterior bands complete or nearly complete across venter; each band solid, without pale central portion. Venter brown without numerous dark flecks and spots .................... *Dipsas sanctijohannis* (Boulenger) (Colombia: western slopes of the Cordillera Occidental in Chocó and the inter-Andean valley of the Río Cauca)

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[7] The elongate blotches on the parietal region in *Dipsas oreas* occasionally fuse to form an irregular V-shaped mark that is very different from the marking in *D. andiana*. See Cadle and Myers (2003: 24, fig. 11).

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## SPECIMENS EXAMINED AND LOCALITY RECORDS

A few literature records are included herein when there is reason to be assured of the identity of the specimens, which is rarely the case with South American species of *Dipsas.* Some of these records are discussed in the above species accounts (see sections on *Distribution*). In addition to specimens of the three species of the *oreas* group, this list also includes material of *D. gracilis, D. latifasciata,* and *D. temporalis* examined during the course of this study. This should aid future workers on this genus because many of the identifications in the literature are questionable and much material has accumulated since the group was last reviewed (Peters, 1960a). Discussion of some apparent problems concerning the systematics of *D. gracilis* and *D. latifasciata* is given in the text. Other material relevant to the identity of species in western Ecuador was listed in Cadle and Myers (2003) (*D. andiana, D. nicholsi,* and *D. variegata*).

Institutional abbreviations for museums are as follows.

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|---|---|
| AMNH | American Museum of Natural History, New York |
| ANSP | Academy of Natural Sciences of Philadelphia |

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| BMNH | The Natural History Museum, London |
| FMNH | Field Museum of Natural History, Chicago |
| KU | Museum of Natural History, University of Kansas, Lawrence |
| LSUMNS | Museum of Natural Science, Louisiana State University, Baton Rouge |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge |
| MUSM[8] | Museo de Historia Natural de San Marcos, Lima, Peru |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| MVZ | Museum of Vertebrate Zoology, University of California, Berkeley |
| UMMZ | Museum of Zoology, University of Michigan, Ann Arbor |

## *Dipsas elegans*

**ECUADOR:** "Tehuantepec" [Oaxaca, Mexico], in error (see text), BMNH 1946.1.21.77 (holotype). "Western Ecuador," BMNH 60.6.16.73. **[Prov. Chimborazo]:** Pallatanga [1,500 m; 01°59′S, 78°57′W], BMNH 80.12.5.267. **Prov. Cotopaxi:** Corazón [900–1,200 m; 01°08′S, 79°04′W], USNM 210938–39.[9] **Prov. Pichincha:** Way to Mindo [0°2′S, 78°48′W], USNM 210934, 210961 (see footnote 9). 2.9 km SW Tandayapa on Mindo Road, 1,820 m [0°1′S, 78°46′W], USNM 285957. Nanegal Grande [about 1,400 m; 0°7′N, 78°40′W], USNM 210936. Below Pacto, [1,200 m; approximately 0°8′N, 78°45′W], USNM 210937. Río Saloya, 4,000 feet [1,220 m; 0°1′N, 78°57′W], BMNH 1940.2.20.32. Santo Domingo de los Colorados [500 m; 0°15′S, 79°9′W], USNM 210935. Perucho [1,830 m; 0°6′N, 78°25′W] (Orcés and Almendáriz, 1987]. El Quinche, 2,640 m [0°6′S, 78°17′W] (Orcés and Almendáriz, 1987). Cumbayá, 2,354 m [0°12′S, 78°26′W] (Orcés and Almendáriz, 1987). Chiriboga, 1,800 m [0°15′S, 78°44′W] (Orcés and Almendáriz, 1987). Tumbaco [2,400 m; 0°13′S, 78°24′W] (Orcés and Almendáriz, 1987). **Prov. Imbabura:** Near Peñaherrera-Intag, 1,500 m [0°21′N, 78°31′W], UMMZ 92073.

## *Dipsas ellipsifera*

**ECUADOR: [Prov. Imbabura]:** Ibarra [=Ybarra; 2,211 m; 0°21′N, 78°7′W], BMNH 1946.1.21.26 (formerly 98.4.28.87) (syntype), BMNH 1946.1.21.27 (formerly 98.4.28.89) (syntype), BMNH 1946.1.21.28 (formerly 98.4.28.88) (syntype), BMNH 1946.1.21.29 (formerly 98.4.28.90) (syntype), MCZ 8431. Lita, 572 m[10] [0°52′N, 78°28′W] (Orcés and Almendáriz, 1987). Chachimbiro, 2,600 m [0°27′N, 78°13′W] (Orcés and Almendáriz, 1987). Pimampiro, 2,000 m [0°30′N, 77°56′W], UMMZ 83697–700.

## *Dipsas gracilis*

**ECUADOR: Prov. Esmeraldas [?Prov. Pichincha]:**[11] Hacienda Equinox, 30 km NNW Santo Domingo de los Colorados, 1,000 ft. [305 m; approximately 0°5′N, 79°8′W], USNM 210945. **Prov. Guayas:** near Guayaquil [approximately 2°10′S, 79°50′W], USNM 210947. **Prov. Pichincha:** 47 km S. Centro Científico Río Palenque, 150–220 m [approximately 0°50′S, 79°30′W], USNM 286478–80. Centinela, 14.1 km SE Patricia Pilar by road, 570–600 m [0°37′S, 79°18′W], MCZ 156894. Santo Domingo de los Colorados [0°15′S, 79°9′W], USNM 286477. Centro Científico Río Palenque [200 m; 0°33′S, 79°22′W], MCZ 147183. Estación Biológica Río Palenque, 56 km N Quevedo, 220 m [0°33′S, 79°22′W], KU 152604.

**PERU: Depto. Tumbes:** Quebrada Los Naranjos, 3°50′S, 80°14′W, 620 m, MUSM 17589.

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[8] MUSM-JEC refers to Cadle field numbers for which the MUSM catalogue numbers are not yet available.

[9] USNM specimens from "Corazón" (USNM 210938–39) and "Way to Mindo" (USNM 210934, 210961) are probably equivalent in whole or in part to EPN 717–718 ("El Corazón") and EPN 719 ("camino a Mindo") cited by Peters (1960a: 92) as "*Dipsas ellipsifera.*" According to USNM records, these specimens were obtained by Peters from Gustavo Orcés-V. and recorded originally as "GOV 717–719" (Steve Gotte, personal communication, October 2004). Orcés-V. was, at the time, curator at the EPN.

[10] I confirmed the elevation of Lita given by Orcés and Almendáriz (1989) on two maps ("República del Ecuador" 1:1,000,000 published by the Instituto Geográfico Militar [Quito], 1991; and "Ecuador" 1: 1,000,000 published by ITMB Publishing, Vancouver, 1994–1996). Paynter (1993) gave 900 m as the elevation.

[11] My maps place this locality, as given by distance from Santo Domingo de los Colorados, in Pichincha Province. The specimen was obtained by James A. Peters, who used "Esmeraldas Province" in his field notes and as registered in the USNM catalogues (S. Gotte, personal communication, September 2004). Data on a paper label within the jar differ slightly from the catalogue data: 32 km NNW Santo Domingo de los Colorados and "James Brown Farm," rather than "Hacienda Equinox."

### *Dipsas gracilis*(?)

**PERU: Depto. Piura:** Provincia Ayabaca, Valle del Río Quiroz [approximately 4°45′S, 79°50′W], MUSM 2700–01.

### *Dipsas latifasciata*

**ECUADOR: Prov. Napo:** Coca [0°28′S, 76°58′W], MCZ 166589–90. El Reventador [approximately 0°40′S, 77°40′W; locality assumed to refer to lower eastern slopes of Volcán El Reventador, a high peak in the eastern cordillera], MCZ 164510–11. 21 km SSW Reventador, 1,700 m [approximately 0°7′S, 77°38′W; Lynch and Duellman, 1980: 85], KU 164212. Lumbaqui [0°3′N, 77°20′W], MCZ 164674–75.

**PERU: [Depto. Cajamarca]:** Tabaconas [1,892 m; 5°19′S, 79°18′W], MCZ 17404. **[Depto. San Martín/Loreto]:** Cumbre Ushpayacu-Mishquiyacu, 3,200 feet [975 m; 6°57′S, 76°3′W],[12] AMNH 52444. **Depto. Pasco:** Playa Pampa, about 8 km NW Cushi on trail to Chaglla, 2,100 m [9°57′S, 75°42′W[13]], LSUMZ 45499.

### *Dipsas oreas*

**ECUADOR:** "The elevated Valley of Quito" (probably southern Ecuador, as discussed in the text), ANSP 10115 (holotype). "Western Ecuador," BMNH 60.6.16.56, 60.6.16.63. **Prov. Chimborazo:** Alausí, 2,390 m [2°12′S, 78°50′W] (Despax, 1911: 36, as "*Leptognathus mikani*"). **Prov. Chimborazo/Cañar:**[14] Huigra to Río Chiguancay [2°13′S, 79°3′W], ANSP 18117, 18120, 18123. [Río] Chanchan Valley [approximately 2°17′S, 79°24′W], MCZ 17083, UMMZ 56491. **Prov. Guayas:** Guayaquil [2°10′S, 79°50′W], USNM 60006, 62797–802. **Prov. Loja:** Catamayo Valley, 9,780 feet [2,982 m; approximately 4°5′S, 79°35′W], USNM 98923. "Loja, Nouvelle-Grenade" [inferred to be the city of Loja, 2,200 m; 4°S, 79°13′W], MNHN 6285 (holotype of *Leptognathus andrei* Sauvage, 1884; see Kofron, 1982: 48–50]. 13 km E Velacruz (20 km NE Catacocha), 2,250 m [3°58′S, 79°33′W], KU 142803.

**PERU: Depto. Piura:** Immediate vicinity of Ayabaca, approximately 2,600 m [4°38′S, 79°43′W], MUSM-JEC 10347. Toronche (town at base of Cerro Aypate), approximately 16 km (airline) SE Ayabaca, 1,950 m [4°35′S, 79°32′W], MUSM 16750. 2 km W Porculla [Pass] [5°51′S, 79°31′W], MVZ 119330. About 15 km (by road) E Canchaque on road to Huancabamba [about 5°24′S, 79°36′W], LSUMNS 27373.[15] **Depto. Cajamarca:** Río Zaña Study Site, 1,450–1,800 m [6°51′S, 79°6′W; see *Materials and Methods* for interpretation of this locality], ANSP 31777–81, 31783–86; FMNH 232570–72, 232575; MUSM 3361, 3452, 5530, 5532–33, 16751–52.

### *Dipsas temporalis*

**COLOMBIA: Depto Chocó:** Agua Clara, Río Tamaná [approximately 4°53′N, 76°45′W], USNM 267244. **PANAMA: [Prov. Panamá]:** Pequeni-Chagres ridge, head of Rio Limpio and Quebrada Las Tres Honeras (Panama snake census) [9°18′N, 79°27′W], MCZ 50214. South slope of Cerro La Campana, 850 m [8°43′N, 79°54′W], KU 110293. **Prov. Darién:** Ridge between Río Jaque and Río Imamadó, 800–890 m [7°35′N, 77°57′W; see Cadle and Myers, 2003: fig. 16], KU 110294–96. North ridge of Cerro Cituro, Serrania de Pirré, 900–1,000 m [approximately 8°5′N, 77°46′W], KU 110298–110301.

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[12] The specimen is part of the Harvey Bassler collections from eastern Peru (see Myers, 2000: 139–141). The locality is along a ridge separating the headwaters of the Río Mishquiyacu (Río Huallaga drainage) and the Río Uchpiyacu (Río Ucayali drainage) and forming the border between San Martín and Loreto departments. The Mishquiyacu flows westward into the Río Huallaga near the town of Pilluana. The Uchpiyacu flows eastward into the Río Cushabatay, a tributary of the Río Ucayali.

[13] Coordinates from Dr. Thomas S. Schulenberg, who collected the specimen.

[14] Lower reaches of the Río Chanchan form the border between Chimborazo and Cañar provinces. Huigra itself is in Chimborazo province.

[15] Another specimen from near Canchaque collected in the early 1990s is in the Museo de Historia Natural de la Universidad Privada Antenor Orrego (Trujillo, Peru). It is referable to *Dipsas oreas* on the basis of color pattern (I examined the specimen briefly in 1994 but did not complete details such as scale counts).

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*NOTE ADDED IN PROOF*: Paulo Passos kindly called my attention to Fernandes et al. (2002), in which *Dipsas latifasciatus* is synonymized with *D. polylepis*. These authors could not resolve the status of *D. polylepis* vis-à-vis *D. latifrontalis*.